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The Consequences of Non-Native Species Invasions on the Contemporary and Historic Trophic Ecology of Native Sport Fish in a Lake Michigan Embayment

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THE CONSEQUENCES OF NON-NATIVE SPECIES INVASIONS ON THE CONTEMPORARY AND HISTORIC TROPHIC ECOLOGY OF NATIVE SPORT FISH IN A LAKE MICHIGAN EMBAYMENT

By

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ABSTRACT

THE CONSEQUENCES OF NON-NATIVE SPECIES INVASIONS ON THE CONTEMPORARY AND HISTORIC TROPHIC ECOLOGY OF NATIVE SPORT FISH IN A LAKE MICHIGAN EMBAYMENT

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The widespread establishment of dreissenid mussels (*Dreissena spp.*) in Lake Michigan has strongly altered energy flow by sequestering nutrients in nearshore benthic habitats. Despite these ecosystem changes, little is known about their influence on resource partitioning in nearshore fish communities. Here we use stable isotope analysis to characterize the contemporary fish community and historic walleye (*Sander vitreus*) population of Lake Michigan's Little Bay de Noc. We found species-specific differences in the $\delta^{15}N$ and $\delta^{13}C$ values for 14 fish species. High degrees of niche overlap between walleye, northern pike (*Esox lucius*), smallmouth bass (*Micropterus dolomieu*) and yellow perch (*Perca flavescens*) indicating shared use of common prey items including round goby (*Neogobius melanostomus*)]. As length increased, northern pike and smallmouth bass increased their reliance on nearshore resources, while walleye increased reliance on pelagic resources. Isotope analysis over a 31-year time series coincident with the invasion of dreissenid mussels suggests that alterations in energy dynamics influencing walleye were dictated by varied responses from dominant prey items. Furthermore, sex-specific differences in walleye spawning movements indicated that females make significantly greater movements than males possibly driven by higher energetic and reproductive demands. This study improves our understanding of the Lake Michigan ecosystem by informing how whole-scale shifts drive trends in important sport fish communities.

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LIST OF ABBREVIATIONS

ANCOVA:	Analysis of covariance
ANOVA:	Analysis of variance
COIL:	Cornell University isotope laboratory
CPUE:	Catch per unit effort
DI:	Deionized
GSI:	Gonadalsomatic index
LBdN:	Little Bay de Noc
MDNR:	Michigan Department of Natural Resources
no.:	Number
sd:	Standard deviation
SEAc:	Size-corrected standard ellipse area
SIA:	Stable isotope analysis
SSD:	Sexual size dimorphism
TA:	Total area
TL:	Total length
Tukey HSD:	Tukey's honest significant difference

CHAPTER ONE: CONSEQUENCES OF INVASIVE SPECIES ON NEARSHORE SPORT FISH IN LITTLE BAY DE NOC

INTRODUCTION

Impacts from overfishing, eutrophication, and non-native species have contributed to altered trophic dynamics across the entire food web in Lake Michigan (Madenjian et al. 2002; Bunnell et al. 2015). The invasion of dreissenid mussels redirected the flow of energy from pelagic to nearshore benthic habitats, which has contributed to decreased pelagic productivity (Hecky et al. 2004; Turschak and Bootsma 2015) and caused many species of fish and benthic invertebrates to increase their reliance on nearshore benthic energy (Turschak et al. 2014). Coincident with declining pelagic production, prey fish biomass has declined (Fahnenstiel et al. 2010; Turschak et al. 2014), reflecting the broader shifts in energy flow mediated by dreissenid mussels.

Dressenid mussels also facilitated the establishment and rapid population growth of the invasive round goby (*Neogobius melanostomus*) (Vanderploeg et al. 2002). Dreissenid mussels have created an ample food supply for round goby as they are directly preyed upon by larger gobies and habitat for the macroinvertebrates preferred by smaller gobies (Vanderploeg et al. 2002; Bunnell et al. 2015). Round goby have altered Lake Michigan's food web dynamics by modifying benthic communities through their consumption of non-dreissenid invertebrates (Barton et al. 2005; Bunnell et al. 2014), facilitating recruitment collapses of native benthic fishes (Janssen and Jude 2001; Corkum et al. 2004), and increasing competition with other species for resources (Bergstrom and Mensinger 2009; Creque and Czesny 2012). However, data also suggest that round goby have become an important diet item to native piscivores [e.g.

smallmouth bass (*Micropterus dolomieu*)] that readily incorporate round goby into their diet (Vanderploeg et al. 2002).

The impact of invasive species on nearshore and embayment food webs has not been studied as extensively as their impact to offshore food webs. This is driven in part by a lack of coordinated lake-wide monitoring programs and cohesive sampling techniques (cf. Bunnell et al. 2014; Fetzer et al. 2017). Nearshore habitats provide anglers and other resource users access to many important sport fish species that utilize these areas for foraging and reproduction (Barbier et al. 2011; Sierszen et al. 2012). Invasive species can drive ecosystem level change in nearshore systems and reduce their ability to provide key ecosystem services including the maintenance of fisheries (Barbier et al. 2011), making the study of these changes a top priority for resource managers (Sierszen et al. 2019). For example, increases in water clarity resulting from the invasion of dreissenid mussels (Bunnell et al. 2014) are expected to negatively affect the production native nearshore sportfish like walleye (*Sander vitreus*), though management actions to compensate for this loss remain uncertain (Lester et al. 2004; Hansen et al. 2019). Furthermore, nearshore zones (< 30m in depth) contain a mosaic of habitat types (e.g., river mouths, wetlands, protected bays) with different physical and chemical attributes that influence fish community structure (Fetzer et al. 2017) and resource use patterns (Sierszen et al. 2019). Due to the heterogeneity that exists both within and among nearshore habitats, a mechanistic understanding of how communities respond to ecosystem disturbances has proved challenging (Fetzer et al. 2017).

Stable isotope analysis (SIA) is a commonly used to assess the trophic ecology of fishes using the ratio of stable isotopes assimilated in an organism's tissues through their diet (Layman et al. 2012). Other assessments of trophic structure based on gut content analysis lack the spatial

and temporal information about an organism's diet that are integrated into stable isotope analyses (Layman et al. 2012). Stable isotope ratios in fishes contain information about the composition their diets and the fractionation of isotopes that occurs during food processing (e.g., digestion and assimilation) (Peterson and Fry 1987). The ratios of ^{13}C to ^{12}C ($\delta^{13}C$) fractionate minimally during trophic transfer (~0‰) and are used to distinguish between sources of available energy, which differ substantially among primary producers (Peterson and Fry 1987). The ratios of ^{15}N to ^{14}N ($\delta^{15}N$) fractionate about 3.4‰ on average with each trophic transfer and can therefore be used to estimate trophic position (Post 2002). Plotted together, $\delta^{13}C$ and $\delta^{15}N$ can be used to depict a species' isotopic niche, which can be used to determine different aspects of trophic structure such as niche space and trophic redundancy (Jackson et al. 2011; Swanson et al. 2015). Additionally, isotope mixing models can be used to estimate the dietary proportions of prey from the isotopes assimilated by consumers (Parnell et al. 2010, 2013; Phillips et al. 2014). When used in combination, stable isotope techniques and diet analysis allow ecologists to compare and describe trophic dynamics within food webs (Mumby et al. 2018).

Little Bay de Noc (LBdN) in Lake Michigan's northern Green Bay is one example of an important embayment fishery that has been impacted by recent non-native species invasions. LBdN contributes to one of the largest recreational fisheries in Michigan's Upper Peninsula with walleye and yellow perch (*Perca flavescens*) being the primary species targeted by most anglers (Zorn and Schneeberger 2011). Dreissenid mussels are responsible for an approximately 50% increase in water clarity in LBdN, which has been linked to declines in the abundance of forage fish species and yellow perch, as well as changes in walleye migration patterns (Zorn and Schneeberger 2011; Zorn and Kramer 2016). Round goby populations grew rapidly after they colonized LBdN in the early 2000's and by 2005 they composed 77% of trawl catches, which led

managers to suspect that they had adversely affected populations of native fishes (Zorn and Schneeberger 2011). However, there is no information related to energy flow in the food web within this embayment.

In this study, we used SIA and diet analysis to determine what resources currently support native sport fish in Little Bay de Noc (LBdN) in light of nonnative species invasions. Our objectives were to (1) describe the food web structure in LBdN using stable C and N isotopes, (2) quantify the diets of native sport fish including walleye, yellow perch, smallmouth bass, and northern pike (*Esox lucius*), (3) characterize niche size and the extent of isotopic niche overlap among these native sport fish, and (4) use stable isotope mixing models informed by empirically collected diet data to characterize ontogenetic shifts in the diets of walleye and yellow perch.

METHODS

Sample collection

Fish were collected from LBdN located in the northernmost waters of Green Bay, Lake Michigan (Table 1). LBdN covers approximately 161 km^2 and has a contour break running along its length that separates shallow areas that are < 3 meters deep, from deeper areas that are between 12-30 m deep (Zorn 2015). All specimens used for characterizing the fish community were collected during August and September of 2018 and 2019. Experimental mesh gillnets were 194 m in length and consisted of two 97 m experimental sections composed of varying mesh sizes ranging from 25.4 to 127 mm stretch mono providing a general sample of the fish community. Following a stratified-random sampling design, nets were set at 26 different locations for a 24-hour sampling period (Fig. 1). Fish were also collected from 18 m experimental mesh monofilament gill nets set in August and September each year at two long-term index locations (Zorn and Schneeberger 2011). Invertebrate samples were collected from June-August of 2019 using a combination of sampling techniques including kick-netting, plankton tows, Ponar grabs, and terrestrial insect nets (Hagg et al. 2012; Herman and Wickman 2016).

Sample Preparation: Stable Isotopes

Various techniques were used to obtain tissue samples from organisms in preparation for SIA. Total length (mm) and weight (g) were recorded for fish prior to sample preparation. In the lab, a small portion dorsal white muscle tissue was dissected. Most invertebrates were

composited to obtain sample masses sufficient for SIA (~0.9 mg). Rusty crayfish (*Orconectes rusticus*) and damselflies (Odonta) were not subsampled; instead, white abdominal and thorax muscle tissues were dissected to produce samples from individuals. For all fish and invertebrate samples, tissues were placed in a glass scintillation vial and dried at 55°C for > 48 hours before they were homogenized into a fine powder using surgical scissors or mortar and pestle.

Sample Preparation: Diet composition

Dietary information from stomach contents was recorded from sport fish collected in 2019. All identifiable matter from the stomach contents for walleye, yellow perch, northern pike, and smallmouth bass were counted and weighed. A cleithra-based identification key (Traynor et al. 2010) was used to identify prey fish to the lowest possible taxonomic level. Invertebrates were identified to lowest possible taxonomic ranking using widely available taxonomic keys for North American fauna.

Sample analysis

Stable isotopes of carbon and nitrogen and C:N ratios of homogenized samples were determined using a Thermo Delta V isotope ratio mass spectrometer interfaced to an NC2500 Elemental Analyzer (Thermo Fisher Scientific, Waltham, MA) located at the Cornell University Stable Isotope Laboratory (COIL). Isotope corrections were performed after every ten samples using a two-point normalization (linear regression) derived from known isotope standards. Standards include internal Deer standard (animal material) and a chemical methionine standard. Stable isotope ratios of N ($\delta^{15}N$) and C ($\delta^{13}C$) were expressed as:

$$\delta^{15}N \text{ or } \delta^{13}C = [(R_{sample}/R_{standard}) - 1] \times 1000$$

where R is the ratio of ^{15}N to ^{14}N or ^{13}C to ^{12}C. The standard deviations for the isotope standards were: internal Deer ($\delta^{15}N$=0.07‰, $\delta^{13}C$=0.22‰) and chemical methionine ($\delta^{15}N$=0.64‰, $\delta^{13}C$=0.49‰). If tissue C:N ratios were >4, $\delta^{13}C$ values were corrected for lipid content using mathematical normalization techniques following Post et al. (2007).

Statistical analyses

A one-way ANOVA with a Tukey multiple comparisons procedure ($\alpha = 0.05$) was used to evaluate species-specific differences in total length, nitrogen, and carbon stable isotope ratios (ANOVA, $\alpha = 0.05$). Additionally, we used ANCOVA to determine if stable isotope ratios were influenced by species identity with the covariate of total length (ANCOVA, $\alpha = 0.05$; c.f., Gerig et al., 2018). We utilized Q-Q plots and Kernel density ridge plots to determine whether the data met the assumptions of both ANOVA and ANCOVA. All analyses were performed using R version 3.6.3 (R Core Team 2020).

Both frequency of prey occurrence and percent biomass were calculated from stomach contents of each sportfish species. Biomass was determined for stomachs containing spiny water flea (*Bythotrephes longimanus*) but individuals were not counted due to the possibility of overestimating their abundance in stomach contents using caudal spines (Parker et al. 2001).

Bayesian elliptical approaches were used to define the niche space and extent of isotopic overlap among the sport fish community (Jackson et al. 2011; Swanson et al. 2015). We calculated the total area (TA) of each species niche to estimate the total extent of their trophic diversity (Layman et al. 2007). The corrected standard ellipse area (SEA_c) of each sportfish

species was calculated to compare their core niche areas using a subset of the data (Jackson et al. 2011). This calculation corrects for smaller sample sizes and controls for differences in sample size among species (Jackson et al. 2011; Jackson et al. 2012). Isotopic overlap was calculated from the probability that an individual from one species was found in another species isotopic region using a Bayesian framework (Swanson et al. 2015). Overlap results were reported using the mean percent overlap between species combinations with 95% credible interval from 10,000 Monte-Carlo simulations.

Bayesian stable isotope mixing models were used to estimate the assimilated diet of each walleye and yellow perch over a 3-4 month period (June-September) in MixSIAR (Stock et al. 2018). Historic diet data collected as part of a long-term survey by Michigan Department of Natural Resources (Federal Aid to Sport Fish Restoration, Grant F-61-R, Study 747) informed model sources that were most likely to contribute to the diets of walleye and yellow perch (T. Zorn, MDNR, unpublished data). Raw stable isotope values from prey species obtained from LBdN were used to inform the models. In the walleye model, alewife (*Alosa pseudoharengus*) were divided into small (<100 mm) and large (>100 mm) size classes due to large differences in their isotopic values (Fig. 2). In the yellow perch model, spiny water flea (*Bythotrephes longimanus)* were not included as a source due to their central position in isospace relative to other prey isotope signatures (Phillips et al. 2014). *Gammarus* sp. and *Hyalella azteca* were combined into one source renamed “amphipods” due to their similar isotopic signatures and ecological niches. Additionally, midge larvae (Diptera: Chironomidae) collected from the immediate nearshore zone (< 4 m) were used in the yellow perch model due to the distinct isotopic signature of detritivorous midges. The trophic discrimination factors used in the model were 3.4‰ (1 sd = 1‰) for $\delta^{15}N$ and 0.4 (1 sd = 1.3) for $\delta^{13}C$ following recommendations by

Post (2002). For both species, a model was run for 1 x 10^6 iterations, with a burn-in of 5 $\times 10^5$ iterations, and thinning every 500 simulations. Model results are reported using the mean and 95% Bayesian credibility intervals.

RESULTS

Food web structure of LBdN

Muscle samples from 186 sport fish, 141 non-game fish species, and 25 invertebrate samples were analyzed for stable isotope ratios from LBdN (Table 1). The results from these analyses were used to characterize the nearshore food web in isotope space for 14 fish species and nine invertebrate taxa (Fig. 3, Table 1). Most of the $\delta^{13}C$ values for these species fell between -22 and -26, which largely bounded our sport fish of interest. Notable exceptions to this pattern included Eurasian ruffe (*Gymnocephalus cernuus*), rock bass (*Ambloplites rupestris*), and black bullhead (*Ameiurus melas*), which exceeded -31‰ $\delta^{13}C$. Mean $\delta^{15}N$ values were highest for white perch (*Morone americana*) (12.6 ± 1.1 ‰) and lowest for spottail shiner (*Notropis hudsonius*) (8.9 ± 0.6 ‰; Table 1).The native sport fish assemblage including walleye, yellow perch, northern pike, and smallmouth bass, had high $\delta^{15}N$ values (>11‰) suggesting they occupy upper trophic level positions (Fig. 3, Table 1). Round goby and alewife, common prey fish to LBdN, were found to have similar $\delta^{13}C$ (10.2, 9.7‰) and $\delta^{15}N$ (-24.6, -23.3‰) values (Fig. 3, Table 1). Invertebrates had $\delta^{15}N$ values less than 8‰ and wide ranging $\delta^{13}C$ values from -32 and -21‰ (Fig. 3). Ephemera mayfly nymphs (*Ephemera* sp.) had the lowest mean $\delta^{13}C$ among the invertebrates sampled (-29.8 ± 2.0), while rusty crayfish had the highest (-22.0 ± 1.2; Table 1).

When considering the sport fish assemblage, we found differences in $\delta^{15}N$ among species (ANOVA, $F_{3,177} = 16.6$, $p < 0.001$, Fig. 4A). Post-hoc tests revealed that walleye (Tukey HSD, $p < 0.001$) and northern pike had similar $\delta^{15}N$ (Tukey HSD, $p = 0.79$) but were higher than yellow perch (Tukey HSD, $p < 0.001$). Smallmouth bass exhibited a wide range in $\delta^{15}N$ and were

different from walleye (Tukey HSD, $p = 0.26$), yellow perch (Tukey HSD, $p = 0.15$), or northern pike (Tukey HSD, $p = 0.07$). Similar to $\delta^{15}N$, we also found species-specific differences in $\delta^{13}C$ (ANOVA, $F_{3,177} = 41.8$, $p < 0.001$). Walleye had higher $\delta^{13}C$ values than northern pike (Tukey HSD, $p < 0.001$) and yellow perch (Tukey HSD, $p < 0.002$). Yellow perch were similar in $\delta^{13}C$ to northern pike (Tukey HSD, $p = 0.81$). Smallmouth bass had higher $\delta^{13}C$ values than northern pike, walleye and yellow perch (Tukey HSD, $p < 0.001$; Table 1).

The isotope ratios of sport fish varied with total length. All native sport fish had a positive relationship between fish TL and $\delta^{15}N$ (ANCOVA, $F_{3, 173} = 32.9$, $R^2 = 0.55$, $p < 0.001$). The slope of the relationship between fish size and $\delta^{15}N$ was similar between walleye and smallmouth bass in comparison to yellow perch and northern pike. Yellow perch $\delta^{15}N$ values increased rapidly as TL increased, indicating rapid change in trophic level with increasing body length, while northern pike increased more slowly (Fig.4B). The slopes of the relationship between TL and $\delta^{13}C$ were inconsistent among species (ANCOVA, $F_{3, 173} = 22.1$, $R^2 = 0.45$, $p < 0.001$, Fig. 4B). The significant yet different relationships potentially indicate changes in resource use as size increases with negative trends suggesting greater reliance on offshore resources and positive trends suggesting greater reliance on nearshore resources. Walleye and smallmouth bass had negative relationships between TL and $\delta^{13}C$, yellow perch had no relationship, and northern pike had a positive relationship (Fig. 4B).

Sport fish niche area and overlap

Results from our Bayesian elliptical approaches revealed variations in niche size and levels of overlap among the sport fish characterized. Convex hull analyses revealed that walleye

and northern pike had similar total niche areas of 11.8 and 11.5 ‰^{2} (Table 1). Yellow perch had the largest total niche area of any species at 27.1 ‰^{2}, which was 136% larger than walleye, 130% percent larger than northern pike, and 984% larger than smallmouth bass (Table 1). Smallmouth bass had the smallest total niche area of the four species at 2.5‰^{2} (Table 1). The amount of niche overlap estimated between the four native sportfish species was variable, but dependent upon the direction of each species comparison (Table 3, Fig. 5). Walleye exhibited the highest level of overlap when compared to other native sport fish. Walleye overlapped 95% with yellow perch, 75% with northern pike, but only 8% with smallmouth bass (Table 3). Yellow perch had 50% niche overlap with walleye, 51% with northern pike, and 2% with smallmouth bass (Table 3). Northern pike had 75% niche overlap with walleye, 93% with yellow perch, and 3% with smallmouth bass (Table 3). Compared to the other species, smallmouth bass were the most isotopically distinct (Fig. 5). Smallmouth bass had 49% niche overlap with walleye, 35% with yellow perch, and 15% with northern pike (Table 3).

Stomach contents

Stomach contents were sampled in September providing a brief "snapshot" of sport fish diets. As such, they may not reflect other seasonally important diet items. In walleye diets, round goby (55%) and alewife (21%) occurred with the highest frequencies (Table 2). Similarly, for yellow perch, round goby was the most frequently observed prey item (59%) followed by rusty crayfish (24%; Table 2). In northern pike diets, yellow perch (13%) and sucker spp. (13%) occurred with the highest frequencies (Table 2). Unknown diet items in northern pike stomachs mainly consisted of partially digested fish parts with no identifiable structures. For smallmouth bass, round goby were observed in the highest frequency (40%; Table 2). In addition, a large

portion of the smallmouth bass diet was classified as unknown diet (60%). However, this material contained what appeared to be crushed, pink-colored, shell like material that is consistent with crayfish exoskeleton. However, no definitive identifiable structures were found (Table 2).

Walleye and yellow perch mixing models

Mixing models indicated that overall the diet of walleye and yellow perch changed across their ontogeny. The mixing model estimated that the dietary proportions of walleye less than 350 mm reflected widespread consumption of small alewife and ephemera mayfly nymphs . As size increased, the dietary proportions of walleye suggested increased piscivory with round goby, alewife, and yellow perch being consumed (Fig. 6). Averaged across size, walleye had higher dietary proportions for ephemera mayfly nymphs and small alewife (<100 mm) than all other diet items (Table 4). Yellow perch exhibited distinct changes in diet as size increased (Fig. 7). Yellow perch <90 mm consumed a large proportion of midge larvae collected from the immediate nearshore zone (< 4 m) and transitioned to ephemera mayfly nymphs and rusty crayfish by roughly 170 mm. As size increased, the dietary proportion of ephemera mayfly nymphs and rusty crayfish declined sharply. At 200 mm, the proportion of amphipods peaked then slowly declined with increasing size while round goby increased (Fig. 7). Averaged across size, yellow perch had higher dietary proportions of ephemera mayfly nymphs and amphipods than all other diet items (Table 4). Due to limitations in the size distributions and similarity in prey isotope ratios we did not develop mixing models for smallmouth bass or northern pike.

DISCUSSION

Nearshore food web structure

We found large isotopic variation in the overall food web of LBdN with native sport fish exhibiting intermediate isotopic signatures. Previous studies of Lake Michigan's food web found distinct isotopic differences between nearshore and offshore habitats (Turschak and Bootsma 2015). In our study, isotopic differences between resource pools (i.e., nearshore and pelagic) were less apparent as many of our nearshore benthic primary consumers (i.e., amphipods and midge larvae) also had intermediate $\delta^{13}C$ signatures. This may result from the diversity of habitats and inputs of energy to a relatively small system. LBdN includes both littoral (<3 m) and pelagic habitats along much of its length resulting from a channel (12-30 m) that runs along the length of the embayment, facilitating the exchange of energy between habitats (Schneeberger 2000; Zorn and Schneeberger 2011). Moreover, six rivers flow into LBdN increasing habitat heterogeneity and providing additional energy sources (Fry 2002; Hoffman et al. 2010). Previous studies have found, isotopic gradients of $\delta^{13}C$, depleted to enriched (i.e., more positive), occur at the interface between river-large water systems (Fry 2002; Hoffman et al. 2010). Mobile consumers likely feed across these isotopic gradients or between habitats integrating multiple sources of energy that may not reflect discrete spatial isotopic patterns (Hoffman et al. 2010; Turschak et al. 2019). In systems with multiple inputs of energy, spatial isotopic patterns exist though differences in feeding strategies and the mobility of consumers can result in isotopic signatures that do not adhere to these patterns, which we hypothesize is occurring in the food web of LBdN.

Large variations in $\delta^{13}C$ values in invertebrate taxa highlight differences in primary sources of energy between littoral, pelagic, and benthic habitats (Vander Zanden and Rasmussen 1999) within LBdN. In lake food webs, sources of energy are differentiated between littoral production which reflects the enriched $\delta^{13}C$ signature of algae (~ -23.8 ‰), and pelagic production which reflects the relatively depleted $\delta^{13}C$ signature of phytoplankton (~-28.4‰) (Vander Zanden and Rasmussen 1999; Post 2002). Compared to pelagic production, benthic habitats have a slightly more depleted carbon signature (~ 30.5‰) due in part to terrestrial inputs of organic matter and respiration, making differentiation difficult (Post 2002). In our study, we relied on known life history characteristics of organisms to determine which habitats most likely contributed to their depleted carbon sources when applicable (Fig. 3). For instance, ephemera mayfly nymphs had the most depleted carbon signature of any invertebrate, which corresponds with the ecology of these burrowing detritivores reliant on benthic energy (Fremling 1967; Edsall et al. 2001). In contrast, rusty crayfish had the most enriched carbon signature of any invertebrate, which may reflect a high proportion of littoral macrophytes in their diet (Wilson et al. 2004; Roth et al. 2006).

The wide range in carbon signatures of non-game fish also reflects differences in habitat utilization or primary sources of carbon. As an example, alewife in our study exhibited considerable isotopic change with size reflecting known shifts in habitat use (Fig. 2B). Previous studies have indicated that adult alewife are more reliant on pelagic resources than small alewife, which reside closer to shore (O'Gorman et al. 2000) and isotopically reflect nearshore resource use (Turschak et al. 2019). The extremely depleted carbon signature exhibited by Eurasian ruffe was characteristic of a third source of carbon, biogenic methane, not typically identified in lake food web studies (Jones and Gray 2011; Ravinate et al. 2010). Ruffe are benthivorous with diets

largely comprised of midge larvae (Ravinet et al. 2010). In deeper benthic areas, midge larvae use microhabitats in the sediment at the oxic-anoxic interface where methane oxidizing bacteria convert methane into biomass which are then grazed on by midge larvae which are then consumed by ruffe (Jones and Grey 2011). This pattern has been observed in the St Louis River Estuary of Lake Superior but has not been documented in Lake Michigan (Gutsch 2017).

Drivers of Niche Overlap and Differentiation in Native Sport Fish

The four species of sport fish studied exhibited considerable isotopic overlap suggesting the assimilation of carbon from multiple sources, consumption of isotopically similar prey, or a combination of both (Hecky and Hesslein 1995; Peterson and Fry 1987). Consideration of changes in ecosystem structure and species-specific ontogenetic shifts provides greater context for our observations.

Changing ecosystem structure

Altered community structure changes the abundance of available prey for sport fish consumption (Vanderploeg et al. 2002). Prey fish abundance and diversity has changed significantly in LBdN following a series of species invasions which have impacted the broader Lake Michigan ecosystem (Bunnell et al. 2014). For example, alewife abundance has declined roughly seven-fold since the early 1990s (T. Zorn, MDNR, unpublished data). By contrast, the abundance of invasive round goby has increased ~166-fold in bottom trawl assessments since detection in 1998 and now accounts for >75% of the annual trawl catch (Zorn and Schneeberger 2011). Other prey fish including johnny darter (*Etheostoma nigrum*), trout perch (*Percopsis*

omiscomaycus), and rainbow smelt (*Osmerus mordax*) have also declined substantially (Zorn and Kramer 2016; Fetzer et al. 2017).

Niche overlap among sport fish could be driven by consumption of a common prey resource such as round goby. Diet data collected from sport fish confirm that round goby are a frequently encountered prey item that represents greater than 50% of the biomass in walleye, yellow perch, and smallmouth bass (Table 2). In addition, maximum overlap for sport fish centers near -25 ‰, which is similar to the carbon signature of round goby (Fig. 5). Evidence from other Great Lakes studies suggest widespread round goby consumption by nearshore sport fishes. In Saginaw Bay, walleye and yellow perch have been found to frequently consume round goby (Truemper et al. 2006; Pothoven et al. 2017). In Lake Erie, round goby supplanted crayfish as the most common prey in smallmouth bass diets (Crane and Einhouse 2016). In southern Lake Michigan, round goby have rapidly expanded since 2005 and became the dominant food item for several sport fish including walleye, northern pike, and smallmouth bass (Hirethota 2015). Widespread consumption of round goby highlights the generalist, and opportunistic feeding strategy of native sport fish in embayments (Crane et al. 2015).

Consumption of round goby by northern pike was not apparent from our diet analysis but may be explained by the high percentage of stomachs that were empty (55%) or had unidentifiable contents (18%). Previous studies have attributed the high frequencies of empty stomachs in pike to their asynchronous feeding behavior, whereby the time between feeding exceeds the length of digestion (Diana 1979). This feeding behavior enables northern pike to rely on stored energy from previously consumed high quality prey items allowing them to forgo frequent foraging (Chapman et al. 1989; Paradis et al. 2008). However, we hypothesize that the passive nature of our sampling may have selected for pike that were more likely to be actively

foraging and had not recently consumed prey. The frequency of large prey items observed in the diet may also reflect the longer digestion time associated with larger prey relative to smaller prey (e.g., round goby; Garvey and Chipps 2012).

Smallmouth bass diets contained high numbers of round goby though they exhibited the lowest amount of niche overlap with other sport fish that consumed round goby. The disparity in diet and isotope data between smallmouth bass and other sport fishes examined may reflect differences in the isotopic composition of goby in the habitats where smallmouth bass foraged and/or the consumption of $\delta^{13}C$-enriched crayfish by smallmouth bass. Round gobies in shallow water habitats (2-5 m) have a significantly more enriched carbon signature compared to those from deeper (8-10 m) habitats resulting from differences in the carbon signatures of their prey, which are more $\delta^{13}C$-depleted in deeper waters (Barton et al. 2005). While this spatial isotopic pattern was beyond the scope of our analysis, it is possible that the enriched $\delta^{13}C$ signature of smallmouth bass could reflect a higher proportion of shallow water gobies in their diet. Similar to our results, Campbell et al. (2009) found that compared to other sport fish smallmouth bass had enriched $\delta^{13}C$ signatures though all species consumed high proportions of round goby, which they attributed a greater reliance on other littoral resources. Alternatively, though not definitively detected in our diet analysis, crayfish are known to be an important prey item for smallmouth bass (Frey et al. 2003; Crane and Einhouse 2016). Therefore, the enriched $\delta^{13}C$ value assimilated from crayfish could also shift the isotopic niche of smallmouth bass away from the area of overlap between sportfish despite high round goby consumption.

Species specific ontogenetic shifts - While shared round goby consumption may largely influence niche overlap among native sport fishes, shifts in diet or habitat use during ontogeny likely drive differences in niche width and position among species (Hammerschlag-Peyer et al. 2011). Prior

studies suggest that large niche areas among sport fishes may encompass ontogenetic shifts in diet and habitat use (Gerig et al. 2018; Mumby et al. 2018). Moreover, the four sport fish in our study showed an increase in $\delta^{15}N$ as TL increased suggesting they were increasing in trophic position with size and potentially consumed larger prey with higher $\delta^{15}N$ concentrations (Peterson and Fry 1987; Cabana and Rasmussen 1994). In addition, the relationship between TL and $\delta^{13}C$ may also reflect changes in habitat or diet as size increases (France 1995; Hecky and Hesslein 1995).

In walleye, $\delta^{13}C$ decreased with size suggesting a shift toward pelagic prey (Fig. 4B). This pattern is also evident in alewife that became depleted in $\delta^{13}C$ with increased size (Fig. 2B). Tag return data also suggests (T. Zorn, MDNR, unpublished data) that walleyes, especially larger females, have shifted their spatial distribution in the last 20 years whereby they move from LBdN after spawning and reside in the deeper more pelagic waters of Green Bay. Consumption of both nearshore benthic and pelagic prey reflect the opportunistic feeding strategy of walleye in LBdN. It is unlikely that increased consumption of yellow perch would account for the observed isotopic relationship due to their low observed frequency in the diet and relatively high $\delta^{15}N$ values. As spiny-rayed fish, yellow perch are not a preferred prey of walleye (Hartman and Margraf 1992; Knight and Vondracek 1993) and in Lake Michigan, walleye feed mostly on soft rayed fish like alewife and rainbow smelt (Schneider et al. 1991).

Yellow perch did not show a directional change in $\delta^{13}C$ as TL increased due to strong ontogenetic shifts in diet that utilize different sources of carbon (Fig. 4B). Previous studies on yellow perch diets in the Great Lakes have indicated a decrease in their reliance on nearshore benthic invertebrates and increased piscivory as size increases (Janssen and Luebke 2004; Parke et al. 2009). In light of our diet and isotopic analyses, we suggest that the non-linear pattern

observed in $\delta^{13}C$ could be explained by transitions in diet from small nearshore benthic invertebrates (midge larvae and amphipods) to larger macroinvertebrates (mainly ephemera mayfly nymphs and spiny water flea) and an increased reliance on round goby at larger sizes (Fig. 4B). Increases in round goby consumption with size have previously been documented in Lake Michigan yellow perch (Truemper et al. 2006; Turschak and Bootsma 2015) and their increasing $\delta^{15}N$ signature with size (Fig. 4A) would also support an increased consumption of higher trophic level prey items. Furthermore, while generally considered and opportunistic predator, Truemper and Lauer (2005) found that yellow perch even selected small round goby over more readily available prey in southern Lake Michigan.

Northern pike displayed an increasing carbon signature as TL increased, likely indicating a greater reliance on nearshore sources of energy at larger sizes. We found that smaller pike had a relatively depleted carbon signature compared to other sport fish, suggesting a higher reliance on pelagic resources (Fig. 4B). We hypothesize that smaller northern pike incorporate seasonally abundant invertebrates (e.g., ephemera mayfly nymphs) in their diets, which could explain their more depleted carbon signature. Northern pike are opportunistic foragers, often consuming prey (aquatic insects, fish, or others) based on their availability and abundance (Craig 2008). Though normally perceived as specialist piscivores, diet studies on northern pike have concluded that invertebrates are often incorporated into their diets and in some cases make up the majority of the prey consumed (Beaudoin et al. 1999; Paradis et al. 2008). Invertebrate consumption by northern pike has also been shown to vary by season, with a majority of invertebrates consumed in the spring when the availability of fish prey is low (Chapman and Mackay 1990; Soupir et al. 2000) and with greater frequency at smaller sizes (Chapman et al. 1989; Beaudoin et al. 1999). At larger sizes pike exhibited more intermediate $\delta^{13}C$ values (~ -24‰) and when coupled with

their high $\delta^{15}N$ values would suggest the consumption of other generalist nearshore sport fish. This conclusion was supported by our diet analysis, which found that all ingested walleye, yellow perch, and smallmouth bass were consumed by pike greater than 600 mm and when combined, contributed to 44% of the diet biomass. Additionally, the walleye, yellow perch, and smallmouth bass have isotopic signatures that would align with this hypothesis. While not apparent in our study, yellow perch are the most frequently consumed prey item of northern pike in many lakes (Chapman et al. 1989; Chapman and Mackay 1990; Beaudoin et al. 1999; Soupir et al. 2000; Paradis et al. 2008). In larger northern pike, high consumption of yellow perch would account for the observed shifts in $\delta^{13}C$ and $\delta^{15}N$ though a larger diet study on northern pike would be needed to reach this conclusion.

Smallmouth bass exhibited a slight decrease in $\delta^{13}C$ as size increased suggesting an increased reliance on round goby or other isotopically similar pelagic prey at larger sizes (Fig. 4B). Smallmouth bass undergo shifts in their diet transitioning from zooplankton and small benthic invertebrates to crayfish and piscivory as size increases (Vander Zanden et al. 1998; Weidel et al. 2000). The smallmouth bass included in our analysis were all over 85 mm in TL and had already undergone these ontogenetic shifts in diet as evidenced by their diet and isotopic signatures. Smallmouth bass are known to become increasingly piscivorous with size (Weidel et al. 2000; Dauwalter and Fisher 2008) and an increased proportion of round goby in their diet at larger sizes may account for the slightly reduced $\delta^{13}C$ and increased $\delta^{15}N$ values. Alternatively, smallmouth bass in Lake Michigan are known to have more extensive movements at large sizes (Kaemingk et al. 2011), possibly covering larger distances and utilizing deeper habitats to feed on pelagic prey, such as rainbow smelt (Cole and Moring 1997). Results from our diet analysis show support the first hypothesis, though the latter or both may be true in LBdN, which might

contribute to the high variability in their isotope signatures. Additionally, a larger sample size of smallmouth bass that included a greater number of smaller smallmouth bass may have increased our ability to characterize their diet and isotopic trends.

Mixing model results

While our mixing models were informed by contemporary and historic diet data, low isotopic variation among sources (i.e., potential diet items), generalist feeding behaviors, and spatial isotopic variability within prey species made them difficult to use. In mixing models, the power to delineate between resources decreases when prey are isotopically similar and/or when habitat specific signatures exist within a prey item (Layman et al. 2012; Phillips et al. 2014). These uncertainties are further exacerbated at upper trophic levels by generalist consumers with intermediate signatures which may be consuming an abundant resource similar in $\delta^{13}C$ or incorporating food items from a wide range of habitats (Hecky and Hesslein 1995). In the absence seasonal diet data, our models were able to show that ephemera mayfly nymphs were an important seasonal resource for walleye and yellow perch early in their ontogeny (Fig. 6 and 7). In addition, our walleye model indicated that small alewife were more important to walleye <350 mm TL, while yellow perch, large alewife, and round goby were potentially more important prey for larger walleye (>350 mm). However, isotopic similarity among the latter three diet items (e.g. goby, large alewife, etc) prevented our model from making precise dietary estimates and limited our ability to determine the relative importance of these prey items individually (Table 4). Our yellow perch model displayed strong ontogenetic shifts in diet as size increased, similar to those found previous diet studies (Parke et al. 2009; Turshack 2015), though dietary estimates of prey items other than ephemera mayfly nymphs were highly uncertain (Table 4). Our exclusion of

spiny water flea as a source (see Methods) likely resulted in the misrepresentation of dietary proportions for other prey items, particularly amphipods (Fig. 7).

Isotope mixing models can be powerful tools for ecologist investigating trophic dynamics (Layman et al. 2012; Phillips et al. 2014), though in our study the lack of distinct isotopic signatures restricted what information could be gleaned from them, highlighting the limitations of their use. Adding additional isotope tracers to our analysis may have provided greater discrimination between energy sources, especially in consumers with ambiguous $\delta^{13}C$ values (Peterson and Fry 1987). For instance, sulfur (S) could be used to distinguish between living and detrital organic matter while hydrogen (H) could be used to identify incorporation of terrestrial organic material contributed through river inputs (Peterson et al. 1986; Doucett et al. 2007). Therefore, including S or H in our isotopic analysis may have helped discriminate between contributions from pelagic and benthic energy sources with similar $\delta^{13}C$ values.

Conclusions

Our analysis revealed that the food web in LBdN is isotopically homogenized and high degrees of overlap were present among important native sport fish. Large ecosystem changes caused by dreissenid mussels (e.g., increasing water clarity and declines in prey fish biomass) and round goby invasion have limited prey availability for higher-level consumers, increasing niche overlap and the potential for competition. Our results support the widespread exploitation of round goby by many economically important nearshore sport fishes and highlight this important trophic linkage in relatively understudied nearshore systems in the Great Lakes region. Furthermore, ontogenetic shifts in diet or habitat preference may drive niche separation among

nearshore sportfish and mitigate the impact of competition. Lastly, this study demonstrates the utility of coupling diet and stable isotope analyses in food web studies to gain insight into systems with complex or altered trophic dynamics.

Table 1. Total length and stable isotope ratios (mean ± sd) of all fish sampled from Little Bay de Noc in 2018. Some invertebrates were composited to obtain sample masses sufficient for stable isotope analysis. TA = total niche area in ‰^{2}. SEA_c = corrected standard ellipse areas in ‰^{2}.

Species	n	Mean TL (mm) ± sd	Mean $\delta^{15}N$ ± sd (‰)	Mean $\delta^{13}C$ ± sd (‰)	TA (‰^{2})	SEA_c (‰^{2})
Sport fish						
Northern pike (*Esox lucius*)	38	592.3 ± 141.4	12.3 ± 0.5	-25.2 ± 1.8	11.8	3.0
Smallmouth bass (*Micropterus dolomieu*)	24	359.0 ± 67.0	11.7 ± 0.5	-20.5 ± 0.8	2.5	0.9
Walleye (*Sander vitreus*)	55	362.9 ± 93.8	12.1 ± 0.7	-23.8 ± 1.5	11.5	2.9
Yellow perch (*Perca flavescens*)	69	172.2 ± 74.2	11.3 ± 1.0	-24.9 ± 1.8	27.1	5.9
Other/prey						
Alewife (*Alosa pseudoharengus*)	13	110.0 ± 33.2	9.7 ± 1.0	-23.3 ± 1.6	--	--
Black bullhead (*Ameiurus melas*)	10	285.6 ± 23.7	10.4 ± 0.4	-29.9 ± 2.0	--	--
White sucker (*Catostomus commersonii*)	14	350.3 ± 124.3	9.6 ± 1.2	-26.1 ± 2.3	--	--
Eurasian ruffe (*Gymnocephalus cernuus*)	16	102.3 ± 18.7	9.3 ± 2.5	-34.3 ± 5.8	--	--
Gizzard shad (*Dorosoma cepedianum*)	18	204.5 ± 124.9	10.8 ± 0.3	-22.7 ± 1.8	--	--
Rainbow smelt (*Osmerus mordax*)	4	123.0 ± 25.0	10.5 ± 0.4	-22.2 ± 0.5	--	--
Rock bass (*Ambloplites rupestris*)	13	143.8 ± 31.2	10.9 ± 1.6	-28.3 ± 3.5	--	--
Round goby (*Neogobius melanostomus*)	20	62.4 ± 13.5	10.2 ± 0.9	-24.6 ± 1.6	--	--
Spottail shiner (*Notropis hudsonius)*	21	102.7 ± 23.6	8.9 ± 0.6	-23.3 ± 2.1	--	--
White perch (*Morone americana*)	12	210.3 ± 41.6	12.6 ± 1.1	-25.6 ± 0.8	--	--
Invertebrates						
Spiny water flea (*Bythotrephes longimanus*)	2	--	8.1 ± 0.0	-25.5 ± 0.0	--	--
Midge larvae (Chironomidae)	4	--	7.0 ± 1.1	-24.0 ± 2.2	--	--
Rusty crayfish (*Orconectes rusticus*)	3	--	8.3 ± 0.6	-22.0 ± 1.2	--	--
Damselflies (Odonta)	3	--	7.6 ± 1.0	-28.9 ± 0.9	--	--
Quagga mussels (*Dreissena bugensis*)	4	--	7.5 ± 0.1	-27.3 ± 0.2	--	--
Gammarus sp.	3	--	6.0 ± 0.4	-24.9 ± 1.0	--	--
Ephemera mayfly nymph (Ephemeridae)	3	--	7.8 ± 1.0	-29.8 ± 2.0	--	--
Hyaella azteca	2	--	5.8 ± 0.1	-26.5 ± 0.1	--	--
Phantom midge (Chaoboridae)	1	--	9.1 ± NA	-25.7 ± NA	--	--

Table 2. Stomach contents of sport fish in Little Bay de Noc given as the biomass (%) and frequency of occurrence (%) of various prey. Unknown diet items included fish parts and other unidentifiable material. Fish were sampled with gillnets in the fall (August – September) of 2019 as part of an ongoing study by the Michigan Department of Natural Resources.

	Northern pike		Smallmouth bass		Walleye		Yellow perch	
Prey	Frequency	Biomass	Frequency	Biomass	Frequency	Biomass	Frequency	Biomass
Rusty crayfish	--	--	--	--	--	--	0.24	0.37
Spiny water flea	--	--	*	0.01	--	--	*	0.35
Ephemera mayfly nymph	--	--	--	--	--	--	0.18	0.01
Zebra mussel	--	--	--	--	0.01	<0.00	--	--
Alewife	--	--	--	--	0.21	0.41	--	--
Emerald Shiner	--	--	--	--	0.01	0.01	--	--
Rainbow Smelt	--	--	--	--	0.04	0.02	--	--
Pumpkinseed	--	--	--	--	0.01	0.05	--	--
Round Goby	0.07	0.01	0.4	0.53	0.55	0.23	0.59	0.26
Yellow Perch	0.13	0.18	--	--	0.05	0.24	--	--
Smallmouth Bass	0.07	0.03	--	--	--	--	--	--
Walleye	0.2	0.23	--	--	--	--	--	--
Sucker spp.	0.13	0.33	--	--	--	--	--	--
Unknown Diet	0.4	0.22	0.6	0.47	0.11	0.04	--	--
Total prey items/biomass (g)	15	554.81	10	23.55	73	386.77	17	65.47
Empty	19		13		56		20	
Not empty	15		10		43		53	
Total stomachs	34		23		99		73	

Table 3. Posterior probability distribution of niche overlap (%). Data displayed represent the mean isotopic overlap between each species combination with the 95% credible interval from 10,000 Monte-Carlo simulations.

		Species B			
Species A		Northern pike	Smallmouth bass	Walleye	Yellow perch
	Northern pike	NA	3 (0-9)	75 (60-88)	93 (84-99)
	Smallmouth bass	15 (1-47)	NA	49 (14-86)	35 (3-84)
	Walleye	75 (60-89)	8 (2-17)	NA	95 (86-99)
	Yellow perch	51 (37-67)	2 (0-6)	50 (37-65)	NA

Table 4. Estimated diet of Little Bay de Noc sport fish via mixing models in MixSIAR. Mean estimated dietary proportion is given along with 95% Bayesian credible interval.

	Estimated prey item proportion	
Species	Walleye	Yellow perch
Amphipods	--	0.31 (0.01, 0.71)
Ephemera mayfly nymphs	0.28 (0.14, 0.47)	0.31 (0.05, 0.69)
Midge larvae	--	0.06 (0.00, 0.27)
Rusty Crayfish	--	0.18 (0.01, 0.56)
Round goby	0.16 (0.00, 0.50)	0.13 (0.01, 0.35)
Small alewife (< 100mm)	0.28 (0.03, 0.54)	--
Large alewife (> 100mm)	0.16 (0.00, 0.48)	--
Yellow perch	0.13 (0.00, 0.42)	--

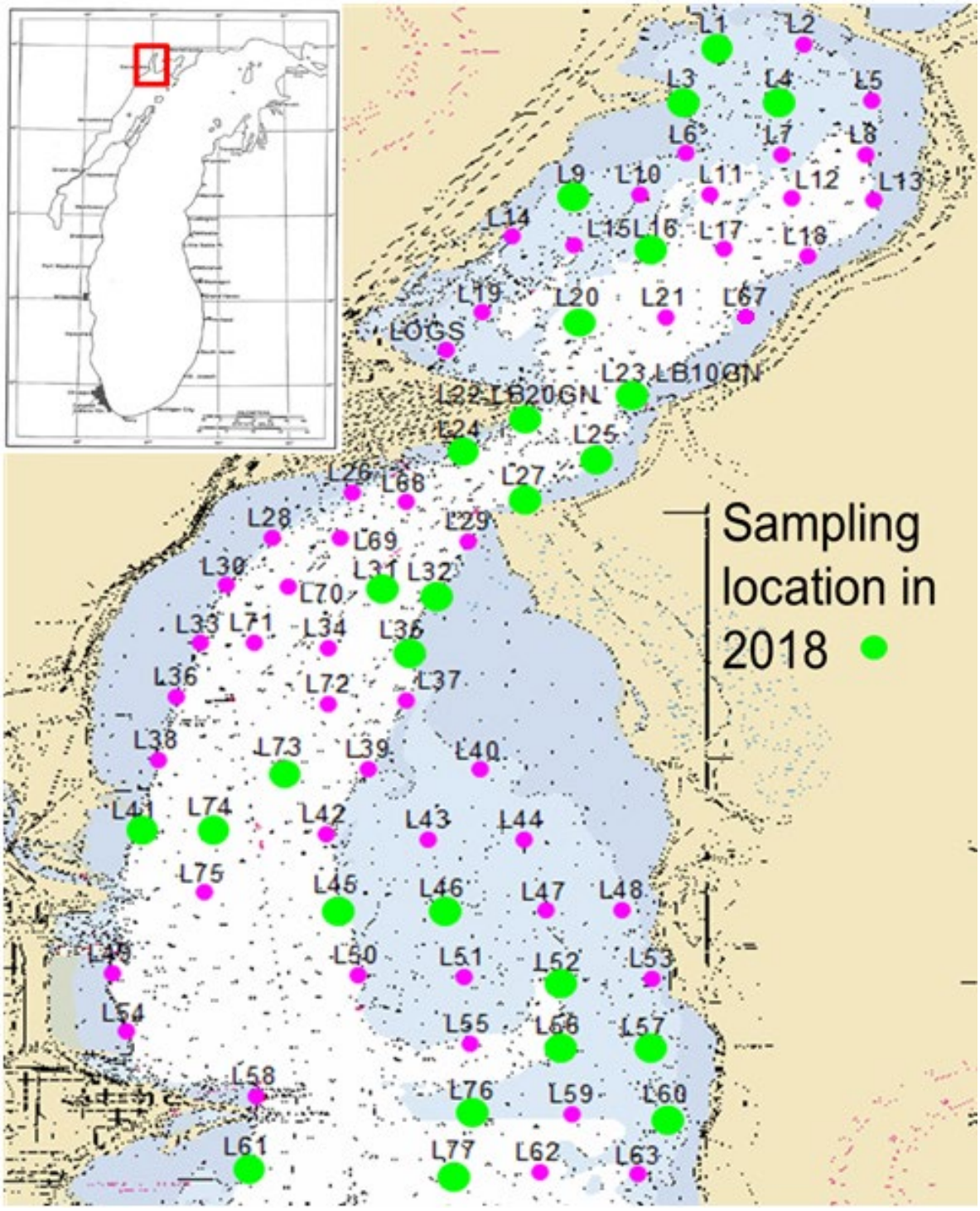

Figure 1. Little Bay de Noc fish sampling sites completed at 26 locations in 2018.

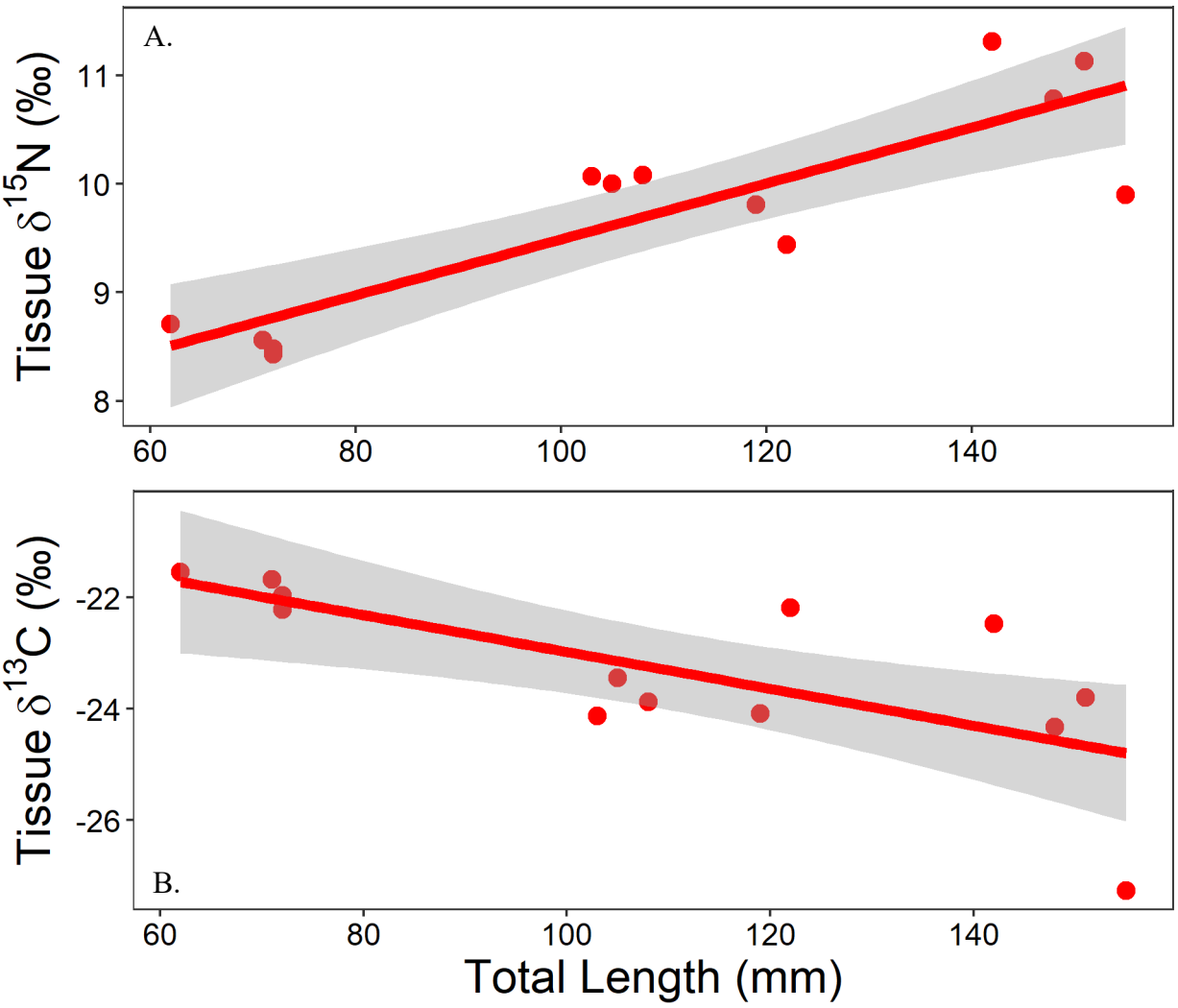

Figure 2. Relationship between total length with (a.) nitrogen and (b.) carbon isotope ratios for alewife (ALE). Large differences in isotope values as size increases allows for smaller alewife (<100 mm) to be distinguished from larger ones (>100 mm).

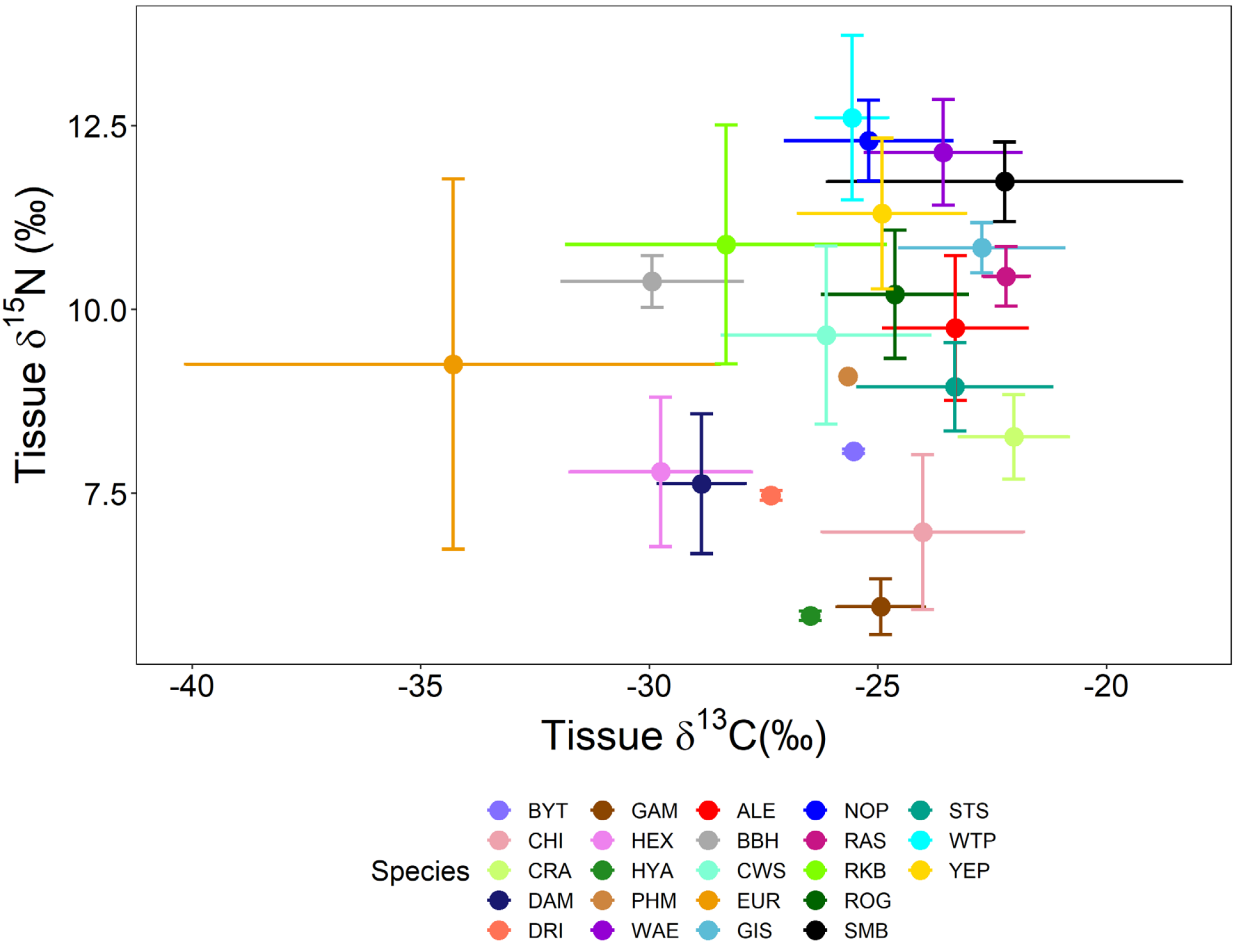

Figure 3. Stable isotope bi-plot of Little Bay de Noc food web represented as the mean ± standard deviation of their stable isotope ratios; BYT = Spiny water flea, CHI = Midge larvae, CRA = Rusty crayfish, DAM = damselfly, DRI = dreissenid mussel, GAM = gammarus, HEX = Ephemera mayfly nymph, HYA = hyalella, PHM = phantom midge, WAE = walleye, ALE = alewife, BBH = black bullhead, CWS = common white sucker, EUR = Eurasian ruffe, GIS = gizzard shad, NOP = northern pike, RAS = rainbow smelt, RKB = rock bass, ROG = round goby, SMB = smallmouth bass, STS = spottail shiner, WTP = white perch, YEP = yellow perch.

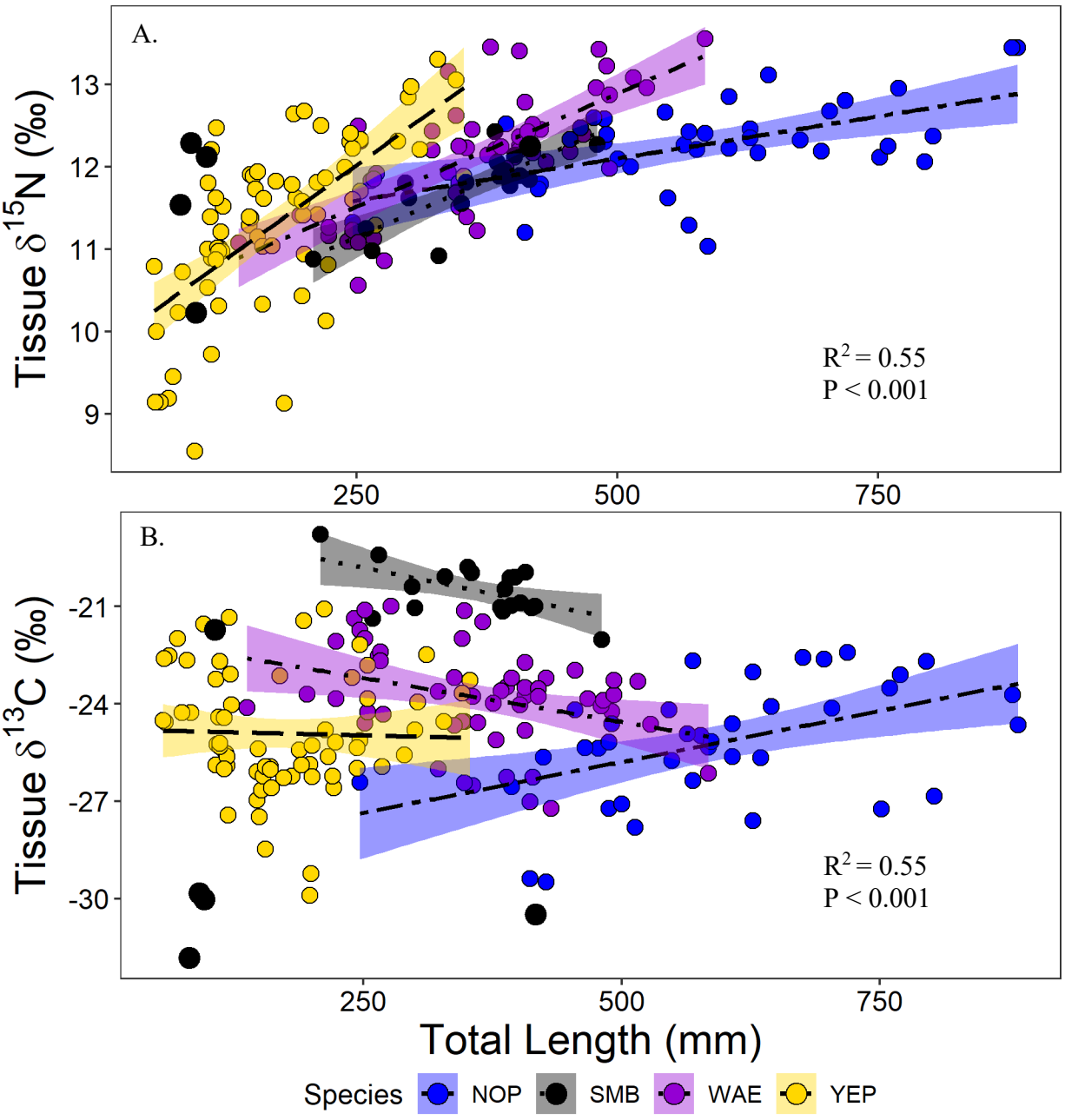

Figure 4. Relationship between total length with (A.) nitrogen and (B.) carbon isotope ratios. NOP = northern pike (two dash), SMB = smallmouth bass (dotted), WAE = walleye (dot dash), YEP = yellow perch (long dash). Lines represent best fish relationship between total length and carbon stable isotope ratios. Shaded areas represent the 95% confidence intervals. R^2 values represent the amount of variance explained and the p-value represents the significance for each model.

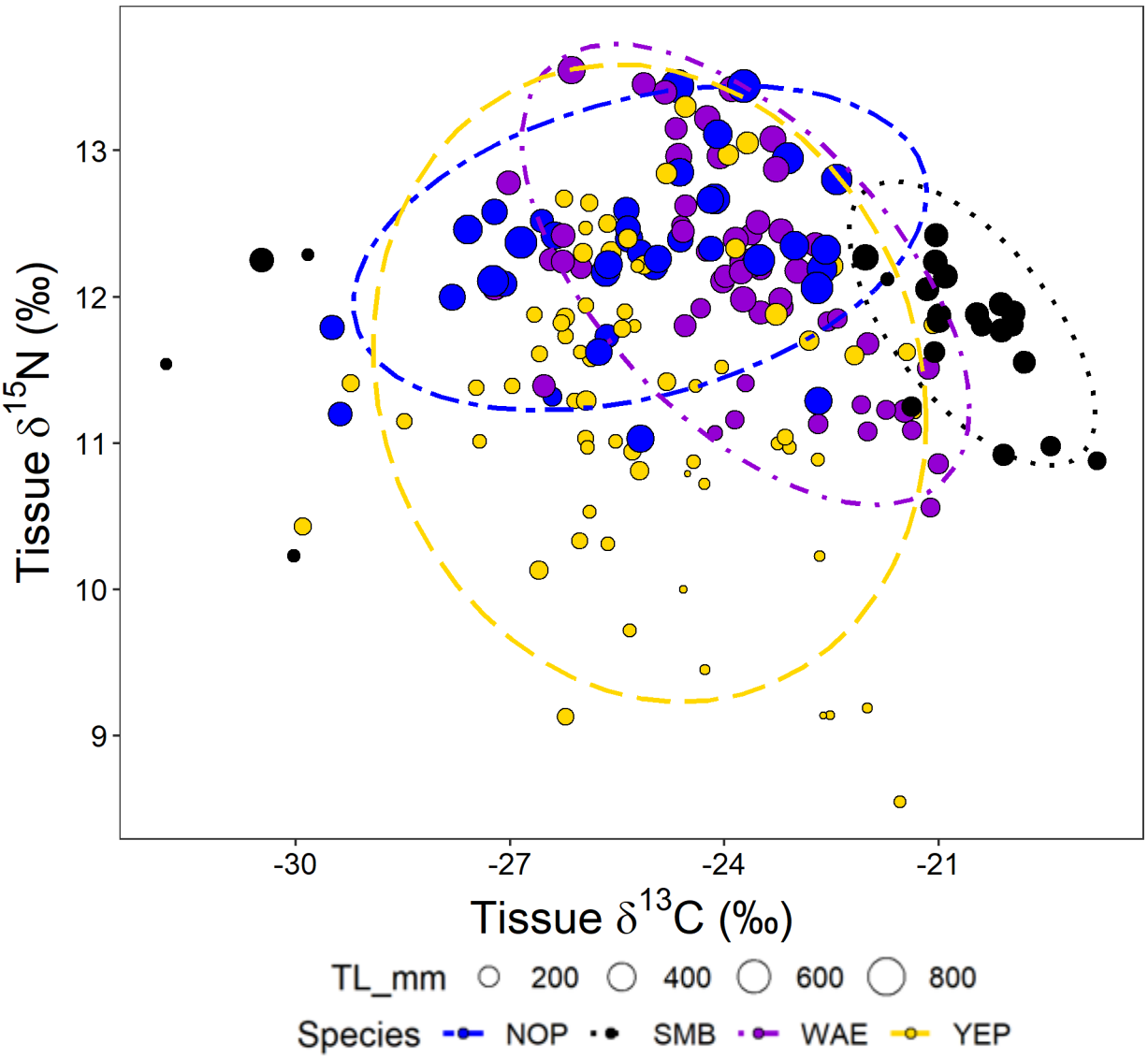

Figure 5. Isotopic niche overlap of predators in Little Bay de Noc. Ellipsoid represents the 95% confidence interval. Size of data point is proportional to total length. Results potentially indicate the convergence on a common prey item, likely round goby, around -25 δ^{13}C. NOP = northern pike (two dash), SMB = smallmouth bass (dotted), WAE = walleye (dot dash), YEP = yellow perch (long dash). Niche size for smallmouth bass is reduced due to the exclusion of 5 outliers, which are present in Figure 3, but do not contribute to the estimation of niche area.

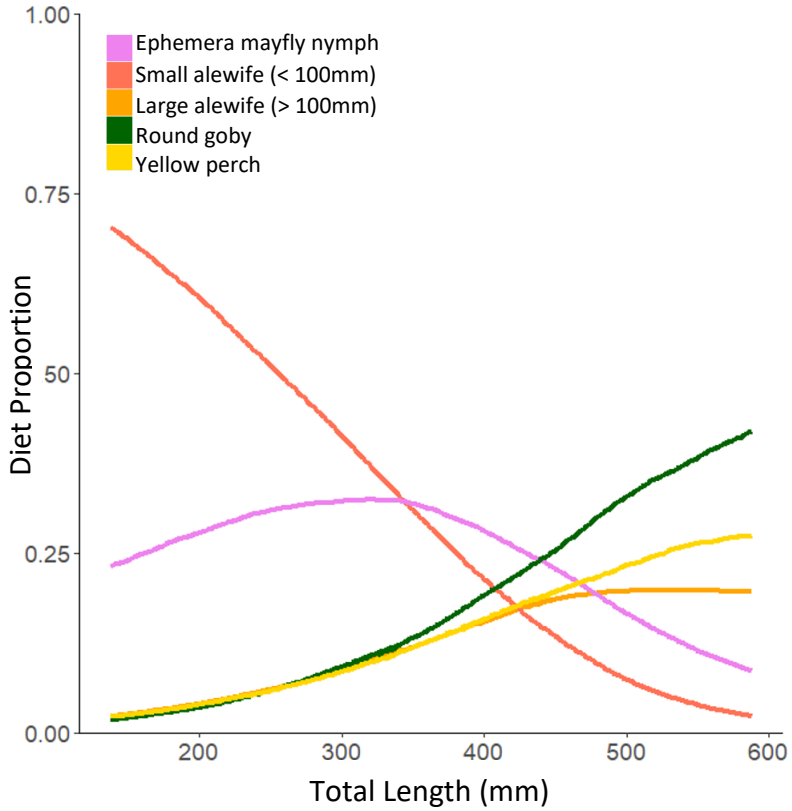

Figure 6. Mean estimated diet proportions as a function of total length from MixSIAR for walleye. Diets of walleye exhibited changes throughout their ontogeny displaying a reliance on small alewife at smaller sizes and higher proportions of round goby in the diet as size increased.

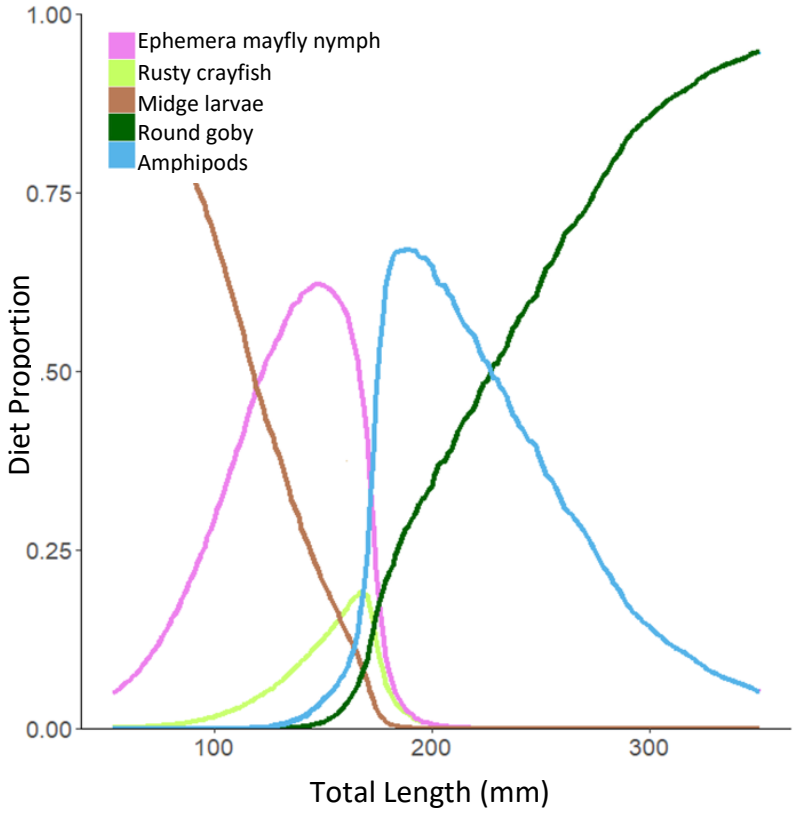

Figure 7. Mean estimated diet proportions as a function of total length from MixSIAR for yellow perch. Diets of yellow perch exhibited changes throughout their ontogeny displaying a reliance on ephemera mayfly nymphs and midge larvae at smaller sizes and higher proportions of round goby in the diet as size increased.

CHAPTER TWO: CHANGES IN THE TROPHIC ECOLOGY AND MOVEMENT OF WALLEYE (*SANDER VITREUS*) FOLLOWING WIDESPREAD ESTABLISHMENT OF DREISSENID MUSSELS

INTRODUCTION

The invasion of dreissenid mussels (*Dreissena polymorpha* and *burgensis*) caused several changes to the energy dynamics of Lake Michigan's food web. After becoming established, filter-feeding activity by dreissenid mussels reduced the transfer of energy to pelagic areas by sequestering nutrients in nearshore benthic habitats, contributing to declines in pelagic productivity (Hecky et al. 2004; Turschak and Bootsma 2015). In response, most fish and non-dreissenid benthic macroinvertebrates increased their reliance on energy derived from nearshore benthic habitats (Turschak et al. 2014), though overall declines in their abundance and biomass reflect the reduced contribution of energy from pelagic production (Zorn and Schneeberger 2011; Bunnell et al. 2014). Other consequences that resulted from the invasion of dreissenid mussels include increases in water clarity as well as declines in water column phosphorus levels and plankton (Bunnell et al. 2014). Recently, studies examining the impact of these ecosystem alterations on fish at higher trophic levels across the Great Lakes have revealed significant changes to their feeding ecology and distribution post invasion (Rush et al. 2012; Fera et al. 2017). However, fish populations from nearshore and embayment habitats have been studied with much less frequency than the pelagic fish community (Fetzer et al. 2017).

Walleye are an economically and ecologically important native apex predator throughout areas of North America where they are native or have been introduced (Schmalz et al. 2011; Pothoven et al. 2017). Historically, the most productive walleye fisheries in North America came from the Great Lakes, including Lake Michigan (Schneider and Leach 1979; Schmalz et al.

2011). Large declines in population levels resulting from overexploitation, pollution, and the impact of invasive species in Lake Michigan led to the banning of commercial walleye fisheries in the late 1970's (Schneider and Leach 1976; Kapuscinski et al. 2010). Further efforts to rehabilitate the walleye population in Lake Michigan through stocking programs, as well as the passing of the Clean Water Act, facilitated the restoration of walleye stocks to levels that supported a popular sport fishery in the 1980's (Kapuscinski et al. 2010). Since then, a wave of invasive species arriving in the ballast water of transatlantic cargo ships have substantially altered the ecosystem in Lake Michigan with wide spread consequences to the fish community (Madenjian et al. 2002; Bunnell et al. 2009).

Walleye populations from Little bay de Noc (LBdN) in Lake Michigan's northern Green Bay have exhibited declines in abundance coincident with the invasion of dreissenid mussels (Zorn and Schneeberger 2011). Historically, LBdN largely contributed to the stock of walleye in northern Green Bay, which at the time was the center of abundance for walleye in Lake Michigan (Schneider and Leach 1976). Today, walleye are the primary target for many anglers in LBdN, which supports the largest recreational fishery in Michigan's Upper Peninsula (Zorn and Schneeberger 2011). Overall, walleye abundance and harvest has declined in LBdN since the 1990's, possibly in response to changing environmental conditions associated with the invasion of dreissenid mussels (Zorn and Schneeberger 2011). Zebra mussels (*Dreissena polymorpha*) became established in LBdN in 1993, though significant changes to the environment were not exhibited until 2002 following the establishment of quagga mussels (*Dreissena burgensis*; Zorn and Schneeberger 2011). Dreissenid mussels are responsible for increases in water clarity in LBdN as well as declines in prey fish abundance (Zorn and Schneeberger 2011; Zorn and Kramer 2016). While the timing of trends in LBdN's walleye population suggests a relationship

with the ecological impact of dreissenid mussels, there is little information connecting these two events.

Biochemical tracers assimilated from the diet, such as the stable isotopes of carbon and nitrogen, are well suited for determining the flow of energy within aquatic systems (Hecky and Hesslein 1995; Layman et al. 2012). The ratios of ^{13}C to ^{12}C ($\delta^{13}C$) fractionate on the order of 1‰ or less with each trophic transfer and used to estimate the relative contributions from sources of available energy, which differ substantially among primary producers (Peterson and Fry 1987). The ratios of ^{15}N to ^{14}N ($\delta^{15}N$) fractionate about 3.4‰ on average, increasing in a stepwise fashion with each trophic transfer making them a useful measurement of consumer trophic position (Vander Zanden and Rasmussen 1999; Post 2002). Dorsal white muscle is the preferred tissue type used by aquatic biologists for analyzing stable isotope ratios in fishes, but often requires sacrificing the individual (Graham et al. 2013). Scales and fin spines offer nonlethal alternatives to muscle tissue and are already commonly collected to gather population and life-history information (Sanderson et al. 2009). Additionally, studies have shown the utility of these alternative tissue types for studying carbon and nitrogen isotope ratios (Syväranta et al. 2008; Hayden et al. 2015). Many research institutions (e.g. agencies, museums, universities, etc.) have large collections of archived scales and fin spines collected by aquatic biologists that could potentially be used to recreate historical food webs and thus, study long-term ecological changes, though surprisingly few studies exist (Syväranta et al. 2008).

In this study, we tested the hypothesis that ecosystem disturbances resulting from invasive species have altered the trophic ecology and movement of walleye in Lake Michigan. The objectives of our study were to (1) compare the trophic status of walleye pre and post-invasion of dreissenid mussels across a 31-year time series using C and N stable isotopes from

archived samples (2) quantify sex-specific differences in walleye movement pre- and post invasion as well as during different return periods, and (3) describe sex-specific differences in walleye size among these periods. We predicted that the stable isotopes of walleye would exhibit lower $\delta^{15}N$ values and an enrichment in $\delta^{13}C$ over time reflecting increased contributions of nearshore benthic energy. Second, we expected that displacement (e.g. movement between tagging and harvest location) would increase with time and be greater for females. Further, we predicted that walleye size would decrease in the post-invasion period and females would be larger than males regardless of invasion or return period.

METHODS

Environmental changes in LBdN

We applied regression analysis to environmental data from LBdN between 1989 and 2018 to identify ecosystem changes coincident with the invasion of dreissenid mussels. Mean density estimates of dreissenid mussels (no./m2) collected every five years by the United States Geological Survey (Nalepa et al. 2014, 2020) were obtained from 6 sampling locations nearest LBdN to identify how environmental variables changed in reference to mussel density. Total prey catch per unit effort (CPUE) data from trawl surveys and secchi disk depth (m) measurements were also obtained from the Michigan Department of Natural Resources (MDNR) Marquette Fisheries Research Station (Marquette, MI) to identify trends in water clarity and prey abundance.

Walleye Tagging

Metal tags were applied to the jaw of walleye that concentrated for spawning near the mouth of the Whitefish River and the northern end of LBdN during April and May. Walleye were captured using conventional fisheries survey methods including boat electrofishing and trap nets (0.91 m high with 38-mm mesh). Biometric data including total length, sex, and date were recorded for each affixed with a tag. The first dorsal spine was also removed to determine age at capture and determine growth between tagging and recapture events. Only walleye of harvestable size (≥ 381 mm total length) were tagged so they would be available for recapture from angler harvest. When tagged walleye were recaptured, anglers were asked to report the tag

number, fish length, date, capture location, and if the fish was kept or released (Schneeberger 2000; Zorn and Schneeberger 2011).

Archived sample collection and preparation

To determine the viability of using archived walleye dorsal spines for stable isotope analysis (SIA) we collected paired samples of dorsal spine and dorsal white muscle tissue from 20 walleye in 2018. Roughly 1 cm of material was collected from the tip of 1-3 dorsal spines per walleye to ensure enough material was obtained for SIA (~0.9 mg). Forceps were used to remove tissue adhered to the spine samples if present. Samples were soaked in deionized (DI) water for approximately 24 hours to remove organic debris and carefully rinsed in fresh DI water upon removal. A small portion dorsal white muscle tissue was also dissected from each of the walleye for comparison. Both tissue samples were placed in a drying oven at 55°C for 48-72 hours after which spines from individual fish were homogenized into a fine powder using a mortar and pestle; muscle samples were homogenized using surgical scissors.

Stable isotopes of carbon and nitrogen and C:N ratios of spine and muscle tissue samples were determined using a Thermo Delta V isotope ratio mass spectrometer interfaced to an NC2500 Elemental Analyzer (Thermo Fisher Scientific, Waltham, MA) located at the Cornell University Stable Isotope Laboratory (COIL). Isotope corrections were performed after every ten samples using a two-point normalization (linear regression) derived from known isotope standards including white-tailed deer and methionine. Stable isotope ratios of N ($\delta^{15}N$) and C ($\delta^{13}C$) were expressed as:

$$\delta^{15}N \text{ or } \delta^{13}C = [(R_{sample}/R_{standard}) - 1] \times 1000$$

where R is the ratio of ^{15}N to ^{14}N or ^{13}C to ^{12}C. The standard deviations for the isotope standards were: White-tailed deer ($\delta^{15}N$=0.07‰, $\delta^{13}C$=0.16‰) and chemical methionine ($\delta^{15}N$=0.65‰, $\delta^{13}C$=0.46‰). If tissue C:N ratios were >4, $\delta^{13}C$ values were corrected for lipid content following Post et al. (2007).

Archived walleye dorsal fin clips were obtained for the years 1988, 1996, 1999, 2002, 2010, and 2019 from the MDNR Fisheries Division. All dorsal spines were collected during the MDNR's annual spring jaw tagging program with the exception of 2010 which were collected during fall gillnet assessment surveys. The years characterized in our analysis coincided with major ecosystem changes that occurred during the dreissenid mussel invasion and had high numbers of sexually mature walleyes represented in the archive. We aimed for a balanced study design where 30 samples of each sex were selected for isotope analysis for the time series. We restricted our analysis to walleye that were 6-7 years of age, presumed to be sexually mature (Zorn and Schneeberger 2011), and relatively similar in size. Additional samples from slightly older or younger age classes were included in some of the years to increase our sample size; however, we treated total length as a covariate to avoid confounding effects between stable isotope ratio and size. Spines from walleye dorsal fin clips were prepared for SIA using the same method outlined previously. Samples from 1988-1999 were used to characterize the pre-dreissenid mussel invasion period in LBdN while samples from 2002-2019 represented the post-invasion period.

Statistical analysis

We evaluated the change in stable isotope ratio and movement between invasion periods using linear mixed-effects models with the *lme4* () package in R version 3.6.3 (Bates et al. 2015, R Core Team, 2020):

Eq. 1: lmer(Stable Isotope Ratio~(Invasion Period*Sex)+Size+(1| Year)

Eq. 2: lmer(ln(Movement +1)~Invasion Period*Sex+Recovery Period +(1| Year)

Eq. 3: lmer(ln(Size)~Invasion Period*Sex*Recovery Period +(1| Year)

Similar to previous research examining the effect of dreissenid mussel establishment on the isotope ratios of fish (Rennie et al. 2009; Fera et al. 2015), our models tested the effect of invasion period while controlling for random variation associated with year. In equation one, to determine if there were sex-specific differences in isotope ratios during each time period, the interaction between fixed factors Sex and Invasion Period was included. Additionally, Size was included as a fixed factor to account for variation in isotope ratios with changes in total length. In equation two, the response variable Movement, or the distance between tagging and recapture locations, was log normalized and interactions among the Invasion Period, Sex, and Recovery Period were included as fixed factors. Recovery Period had two factor levels, "Cold" (November-May) and "Warm" (June-October). These periods were used distinguish between times of the year when walleye were assumed to be allocating energy towards growth or reproduction (i.e., increased productivity and warmer water temperatures) from months with limited energy availability (i.e., lower productivity and colder water temperatures) (Hurley 1986). To investigate sex-specific differences in size between invasion and recovery periods, in

equation three we log normalized Size as our response variable and included interactions among fixed factors Invasion Period, Sex, and Recovery Period.

RESULTS

Environmental change in LBdN

Dreissenid density, total prey CPUE, and secchi disk depth were all found to increase over time (Fig. 8). For dreissenid density (Fig. 8A, R^2=0.38, P=0.16) we were limited to five data points due to the five year cycle with which the USGS takes their measurement though mean mussel density appeared relatively low (693/m^2) in 2000 then increased roughly 8-fold by 2005 (Fig. 8A). Prey CPUE (Fig. 8B, R^2=0.02, P=0.21) and secchi depth (Fig. 8C, R^2=0.13, P<0.05) measurements were highly variable among years. Based upon our regression, total prey CPUE has doubled since 1989 though rapid increases after 2002 mark the invasion of round goby (*Neogobius melanostomus*; Fig. 8B). Secchi disk depth significantly increased over time by roughly 32% (Fig. 8C).

Stable isotopes pre- and post-dreissenids

Our tissue comparison revealed that the $\delta^{15}N$ and $\delta^{13}C$ signatures were strongly related between the two tissues ($\delta^{15}N$, Fig. 9A, $R^2 = 0.78$, $P < 0.001$; $\delta^{13}C$, Fig. 9B, $R^2 = 0.95$, $P < 0.001$). Spine isotope signatures were consistently depleted in $\delta^{15}N$ and enriched in $\delta^{13}C$ relative to muscle [Fig. 9A, $\delta^{15}N_{muscle} = 3.55 + (0.76 \times \delta^{15}N_{spine})$; Fig. 9B $\delta^{13}C_{muscle} = -8.64 + (0.76 \times \delta^{13}C_{spine})$]. The linear isotope relationships between muscle and spine tissue were applied to the $\delta^{15}N$ and $\delta^{13}C$ values of our archived spines as a correction factor, allowing us to effectively use the archived spines as a proxy for dorsal muscle tissue (Table 5).

Analysis of archived fin spines revealed significant changes in walleye isotopic signatures between pre- and post-invasion time periods (Fig. 10 & 11). $\delta^{15}N$ declined sharply by 1.1‰ from the pre to post invasion period (Fig. 10). Based upon the analysis of fixed effects from our mixed model (Eq. 1), an interaction was present between invasion period and sex (t-value=-2.35, P=0.02) indicating that males had higher $\delta^{15}N$ than females prior to invasion but lower $\delta^{15}N$ compared with females post invasion (Fig. 10). However, sex-specific differences were much smaller than the magnitude of difference between invasion periods. In addition, $\delta^{15}N$ increased with walleye size (t=4.1, P<0.001) across both time periods. Overall, the fixed effects explained 47% of the variance while the random effect (1|Year) accounted for 29% of model variance.

The $\delta^{13}C$ increased by 1.2 ‰ from the pre to post invasion period (Fig. 11). An interaction, based upon the analysis of fixed effects from our mixed-effects model (Eq. 1), was evident between invasion period and sex (t-value=2.66, P=0.008) indicating that males were less enriched compared to females post-invasion. Similar to $\delta^{15}N$, sex-specific differences were much smaller than the magnitude of difference between invasion periods. Moreover, like $\delta^{15}N$, $\delta^{13}C$ increased with walleye size (t=4.7, P<0.001). Overall, the fixed effects explained 29% of the variance while the random effect (1|Year) accounted for 15% of model variance.

Sex-specific differences in movement and size

Walleye movement, based upon tag recovery data, increased by 163% from a mean of 8 km pre- to 21 km post dreissenid invasion (Fig. 12) with the frequency of movements exceeding 50 km increasing by 6.75 fold. Based upon the analysis of fixed effects from our mixed model

(Eq. 2) a three-way interaction between invasion period, sex, and recovery period was evident (t-value=-4.46, P<0.001). This interaction indicated that movement was similar between male and female walleye during the cold-water period, while female movement was much higher than males (average displacement 42.9 vs. 13.5 km) during the warm-water tag recovery period post-invasion (Fig. 11, Table 5). Overall, the fixed effects explained 9% of the variance while the random effect (1|Year) accounted for 2% of model variance.

Further analysis of tag recovery data, revealed consistent differences in size between sexes, with females being 30% larger than males on average (Table 5). The analysis of fixed effects from our mixed model (Eq. 3) revealed a marginal three-way interaction between invasion period, sex, and return period (t-value= -1.87, P=0.06) though the magnitude of the differences were generally small (<4%;Table 5). For females, average size was slightly larger during the cold-water period and greater post-invasion (Table 5). Males exhibited similar trends except pre-invasion size was slightly larger during the warm-water period. Additionally, male size during the cold-water period exhibited the largest change overtime, increasing 7.5% post-invasion (Table 5). Overall, the fixed effects explained 41% of the variance while the random effect (1|Year) accounted for 3% of model variance.

DISCUSSION

Environmental changes in LBdN reflect broader ecosystem change that is present in the Great Lakes (Bunnell et al. 2014). Filter feeding activity by dreissenid mussels has limited the flow of energy between nearshore and offshore pelagic zones by sequestering nutrients in nearshore and midwater benthic habitats (Hecky et al. 2004; Vanderploeg et al. 2010). The impact of this redistribution in energy has been linked to basin wide declines in prey fish abundance, water column phosphorus levels, phytoplankton, zooplankton, and non-dreissenid benthic macroinvertebrates as well as increases in water clarity (Cuhel and Aguilar 2013; Bunnell et al. 2014). As we have shown in LBdN, similar impacts from the establishment of dreissenid mussels can observed at smaller spatial scales. The significant increase in water clarity observed in LBdN as evidenced by increasing secchi disk depth, is likely a conservative estimate on the total change in water clarity due to sampling methods (Zorn and Schneeberger 2011). Average annual water clarity estimates were calculated from measurements taken twice a month from July-September during the MDNR fall gillnet surveys (T. Zorn, MDNR, unpublished data). Variations in abiotic conditions (i.e., wind, rain, turnover events) that influence turbidity during the days these measurements were taken may not accurately characterize the true magnitude of change over time. Moreover, the increase in prey fish abundance estimated from trawl CPUE data do not portray recent declines in species diversity or the rapid proliferation of invasive round goby (Fig. 8B). By contrast, the establishment of dreissenids likely facilitated the rapid proliferation of round goby by providing them with ample food resources (Vander Zanden and Rasmussen 2002). Round goby abundance in LBdN has increased ~166-fold in bottom trawl assessments coincident with the invasion of dreissenid mussels and now accounts for >75% of

the annual trawl catch (Zorn and Schneeberger 2011). Additionally, competition between round goby and other native benthic fish for resources has likely contributed to substantial declines in species like johnny darter (*Etheostoma nigrum*) and trout perch (*Percopsis omiscomaycus*) (Malone 2016; Zorn and Kramer 2016). Declines in the abundance of rainbow smelt (*Osmerus mordax*) and alewife (*Alosa pseudoharengus*) in LBdN were reported from 1989-2005 and attributed to less suitable foraging conditions as a result dreissenid mussels and an increasingly oligotrophic water column (Zorn and Schneeberger 2011). Similar declines in open-water planktivores were also observed in Saginaw Bay after dreissenids became established in the early 1990's (Fielder and Thomas 2006). Significant temporal changes in environmental conditions and shifts in prey availability have altered trophic dynamics throughout the Great Lakes (Vanderploeg et al. 2002; Rush et al. 2012). Overall, there is a paucity of information describing how ecosystem changes resulting from dreissenid mussels have impacted fish at higher trophic levels (Bunnell et al. 2014), especially for nearshore fish communities (Fetzer et al. 2017).

Changes in isotope ratios post-invasion

Changes in walleye isotope ratios over time reflect major alterations to energy pathways. Enrichment in $\delta^{13}C$ values by both sexes during the post-invasion period suggest an overall increased reliance on nearshore energy while their declines in $\delta^{15}N$ are more difficult to interpret. Walleye $\delta^{13}C$ increased by ~1.2‰ post-invasion indicating a greater reliance on nearshore resources; nearshore sources of energy have enriched (i.e., more positive) $\delta^{13}C$ signatures compared to pelagic sources (Vander Zanden and Rasmussen 1999; Post 2002). The carbon isotope fractionates minimally during trophic transfer allowing changes in basal energy sources to be interpreted for higher level consumers (Peterson and Fry 1987; Turschak et al. 2014). Two

potential mechanisms describing increases in the $\delta^{13}C$ values of Great Lakes fish post-dreissenid invasion have been identified (Rennie et al. 2009; Fera et al. 2017). First, Rennie et al. (2009) observed enrichment in $\delta^{13}C$, which was attributed to increased nearshore feeding by lake whitefish (*Coregonus clupeaformi*) in Lake Huron. Second, lowered pelagic productivity after the invasion of dreissenids in Lake Michigan, corresponded with increased resource subsidies from nearshore benthic to offshore habitats that were previously reliant on pelagic production (Turschak et al. 2014). This shift is evident across multiple trophic levels and habitat boundaries (Rennie et al. 2013; Turschak et al. 2014). While we are not able to unequivocally identify the mechanism responsible for the apparent shift in $\delta^{13}C$ values in our study, we speculate that the latter is more feasible due to observed increases in walleye movement and relative similarity in isotope ratios between sexes.

Declines in $\delta^{15}N$ exhibited by walleye are more difficult to characterize using the mechanisms proposed for $\delta^{13}C$. Unlike carbon isotopes, nearshore energy is lower in $\delta^{15}N$ compared to pelagic energy (Vander Zanden and Rasmussen 1999; Rennie et al. 2009). Thus, an increase in nearshore foraging by walleye is a potential mechanism driving this isotope trend but would not align with observed increases in movement (Rennie et al. 2009; Fig. 10). Fera et al. (2017) speculated that declines in $\delta^{15}N$ values exhibited by some lake whitefish populations in parts of the Great Lakes could reflect a reduction in food web length due to increased benthic production. While this mechanism is plausible, it would suggest that broad declines in $\delta^{15}N$ should be present for other species, which is not supported by temporal isotope trends (Turschak et al. 2014). Alternatively, we suggest that overall isotope trends exhibited by walleye in LBdN reflect the species-specific responses of important prey fish to changing environmental conditions. For example, recent diet studies on walleye have shown that alewife and round goby

are make up more than 75% of the diet by frequency in LBdN (Whitinger et al. in review). Isotope trends in Lake Michigan from 2002-2003 and 2010-2012 revealed that alewife became depleted in both nitrogen and carbon suggesting an increase in their reliance on zooplankton (Turschak et al. 2014), contrasting trends exhibited by most other fish which increased reliance on nearshore benthic energy. Additionally, round goby exhibited the greatest isotopic change over this time period becoming significantly enriched in $\delta^{13}C$ (~3‰) with minimal changes in $\delta^{15}N$ (Turschak et al. 2014). Taken together, the shift in isotopic ratios we observed for walleye reflects isotopic change in the dominant prey items. Our study highlights that the observed isotopic shift of an apex predator over an ecological disturbance represents both the totality of their trophic interactions over time and the diverse responses of other organisms lower in the food web (Peterson and Fry 1987; Post 2002). Sex-specific differences in isotopic ratios were less apparent compared to overall temporal changes, though they may reflect bioenergetics differences not captured in the stable isotope analysis.

Female movement, bioenergetics, and habitat

The larger movements exhibited by female walleye from LBdN may reflect greater post-spawn energy demands for reproduction relative to males. Studies examining walleye movement using similar tagging datasets from Saginaw Bay in Lake Huron and Lake Erie have also reported sex specific movement patterns showing mature female walleye travel greater distances than males (Wang et al. 2007; Fielder 2016). Moreover, spatial and temporal trends in prey abundance have been identified as a likely driver for movement patterns by mature walleye which have higher energetic needs after spawning (Bowlby and Hoyle 2011). Biphasic growth models which account for sex-specific differences in reproductive investment after maturation

show that males have an asymptotic size that is 25% lower than females (Rennie et al. 2008; Bozek et al. 2011). Two potential mechanisms have been used to explain sexual size dimorphism (SSD) and apparent differences in energy use for walleye, both recognizing that investment in gonadal development and consumption is higher in females (Roff 1983; Henderson et al. 2003). The first asserts that male walleye have lower growth efficiency after maturation due to energy expenditure from higher activity (i.e., movement) while competing with each other for spawning females (Henderson et al. 2003; Madenjian 2011). Alternatively, the second potential mechanism suggests that after maturity the growth rate in male percids [i.e., walleye and yellow perch (*Perca flavescens)]* slows due to both lower feeding activity and gonadal investment resulting in a smaller asymptotic size (Roff 1983; Rennie et al. 2008). Gonadal investment in female walleye, as measured by the gonadosomatic index (GSI), is ~12% higher than males (Malison and Held 1996) and the production of eggs is a more energetically taxing process than spermatogenesis (Bozek et al. 2011). Therefore, female walleye may move greater distances and exhibit higher consumption rates to replenish energy reserves required for future reproductive bouts (Wang et al. 2007; Bowlby and Hoyle 2011). Research from Lake Erie suggests mature female walleye exhibit larger directed movements post spawn from the western to the eastern basin corresponding to increased prey abundance and lower metabolic costs associated with cooler water temperatures (Wang et al. 2007). In Saginaw Bay, higher proportions of large female walleye emigrate out of the bay during periods of high density, which is thought to be driven by a pursuit for greater prey resources beyond the bay (Fielder 2016). Movement data from our study, as well as other Great Lakes walleye populations, show support the latter theory to explain SSD in walleye. Accordingly, these data suggest that lower metabolic demands in mature males do not require them to move or forage as much as females much after spawning

because the energy required to produce sperm is small and not limited by size (Roff 1983; Henderson et al. 2003). Moreover, female walleye may also exit LBdN after spawning to more productive waters in Green Bay searching of better foraging conditions to increase their consumption and ultimately their fecundity (Wang et al. 2007; Zorn and Schneeberger 2011).

Changes resulting from dreissenid mussel establishment have influenced the thermal-optical foraging habitat of walleye, which is reflected by increases in female movement during the post invasion period. Habitats providing walleye with cooler water temperatures, to facilitate optimal growth efficiency, and preferred low light intensities for foraging, are in decline due to increases in water clarity resulting from dreissenid mussels (Lester et al. 2004; Hansen et al. 2019). Optimal temperatures for growth decrease with size for walleye and studies have suggested that movements by larger walleye are influenced by fluctuations in water temperature (Kershner et al. 1999; Hurley 1986). For example, in Lake Ontario's Bay of Quinte, the amount of thermal-optical habitat area has decreased by 34.05 ha/ year in the upper section of the bay since the invasion of dreissenid mussels and increased the proportion of mature walleye in lower parts of the bay (Chu et al. 2004; Bowlby and Hoyle 2011). Based on increases in water clarity, the LBdN ecosystem has become increasingly oligotrophic, which has likely impacted the amount of suitable habitat for the prey community as well. A strong productivity gradient exists in Green Bay with hypereutrophic conditions in the southern portion of the bay, as a result of high nutrient inputs from the Fox river, that become increasing oligotrophic moving north towards LBdN (Padilla et al. 1996; De Stasio et al. 2008). Conditions in the southern portions of the bay support a larger population of pelagic prey due to increased phytoplankton productivity (Brazner and Beals 1997; De Stasio and Richman 1998). Therefore, increasingly oligotrophic conditions in the northern bay resulting from the impacts of dreissenid mussels may have

facilitated a recent shift in the distribution of alewife and other pelagic prey further south. Additionally, round goby have been shown to be energetically poor compared to similarly size prey items preferred by walleye (e.g., alewife and rainbow smelt; Johnson et al. 2005). Taken together, decreases in foraging habitat and the spatial shift of higher quality food items to more productive southern waters, may account for greater seasonal movements exhibited by large female walleye out of the LBdN. By contrast, lower energetic and reproductive demands in male walleye may not require them to make large foraging movements, as they are more capable of persisting on resources within LBdN. The proliferation of round goby throughout Green bay is unlikely to have affected the distribution of walleye in LBdN as round goby are widely dispersed (>25-130m; Mychek-Londer et al. 2013; Pothoven 2018) and would not create a significant spatial contrast to affect overall walleye movements (Bowlby and Hoyle 2011).

Conclusions

The invasion of dreissenid mussels has caused broad environmental changes throughout the Great Lakes (Bunnell et al. 2014), altered the flow of energy between habitats (Hecky et al. 2004), and subsequently caused community wide shifts in resource use (Turschak et al. 2014). Our study illustrates how whole-scale shifts in the ecosystem resulting from non-native species invasions can alter resource dynamics at higher trophic levels. Additionally, demonstrating that fin spines can act as isotopic proxies for muscle tissue in isotope studies provides a tremendous impetus to conduct retrospective analyses of archived material to determine temporal changes in food web structure resulting from species introductions across ecosystems. Slight increases in $\delta^{13}C$ values from walleye over a 31-year time series suggest an increase in nearshore energy subsidies to pelagic communities (Turschak et al. 2014) though declines in $\delta^{15}N$ indicating

increases in nearshore foraging did not align with trends in walleye movement. The mechanism used to characterize trends exhibited in our isotopic analysis highlight that responses to ecological disturbance made at lower levels of the food web ultimately influence the response taken by organisms near the top. Furthermore, our study described how sex-specific differences in bioenergetics, declines in suitable walleye habitat, and productivity gradients in Green Bay potentially account for significantly different temporal patterns in movement exhibited by male and female walleye. The implications from this study will better inform fisheries managers of the impact of invasive species on walleye stocks throughout the Great Lakes and help predict their potential impacts.

Table 5. Sex-specific stable isotope ratios, total length, and displacement (mean ± sd) of Walleye. Values are separated by invasion and return period when applicable. Displacement = the linear distance between tagging and recovery locations. Recovery Period had two factor levels, "Cold" (November-May) and "Warm" (June-October).

Isotopes						
Invasion Period		Sex	Mean $\delta^{15}N$ ± sd (‰)	Mean $\delta^{13}C$ ± sd (‰)	Mean TL (mm) ± sd	n
Pre		Female	13.5 ± 0.3	-24.1 ± 0.4	567.5 ± 44.8	88
		Male	13.6 ± 0.5	-24.3 ± 0.7	518.5 ± 56.1	86
Post		Female	12.5 ± 0.7	-23.5 ± 0.6	561.6 ± 67.4	94
		Male	12.3 ± 0.7	-23.6 ± 0.6	480.7 ± 45.9	95
Jaw tagging						
Invasion Period	Return Season	Sex	Mean Displacement (km) ± sd		Mean TL (mm) ± sd	n
Pre	Cold	Female	5.6 ± 7.2		656.9 ± 78.8	147
		Male	4.9 ± 9.8		488.9 ± 73.1	534
	Warm	Female	7.4 ± 12.4		642.5 ± 65.4	145
		Male	6.5 ± 8.9		498.8 ± 66.0	715
Post	Cold	Female	12.8 ± 26.1		681.2 ± 77.4	235
		Male	5.7 ± 11.3		525.5 ± 83.7	476
	Warm	Female	42.9 ± 39.1		665.6 ± 79.0	102
		Male	13.5 ± 19.9		507.5 ± 86.9	308

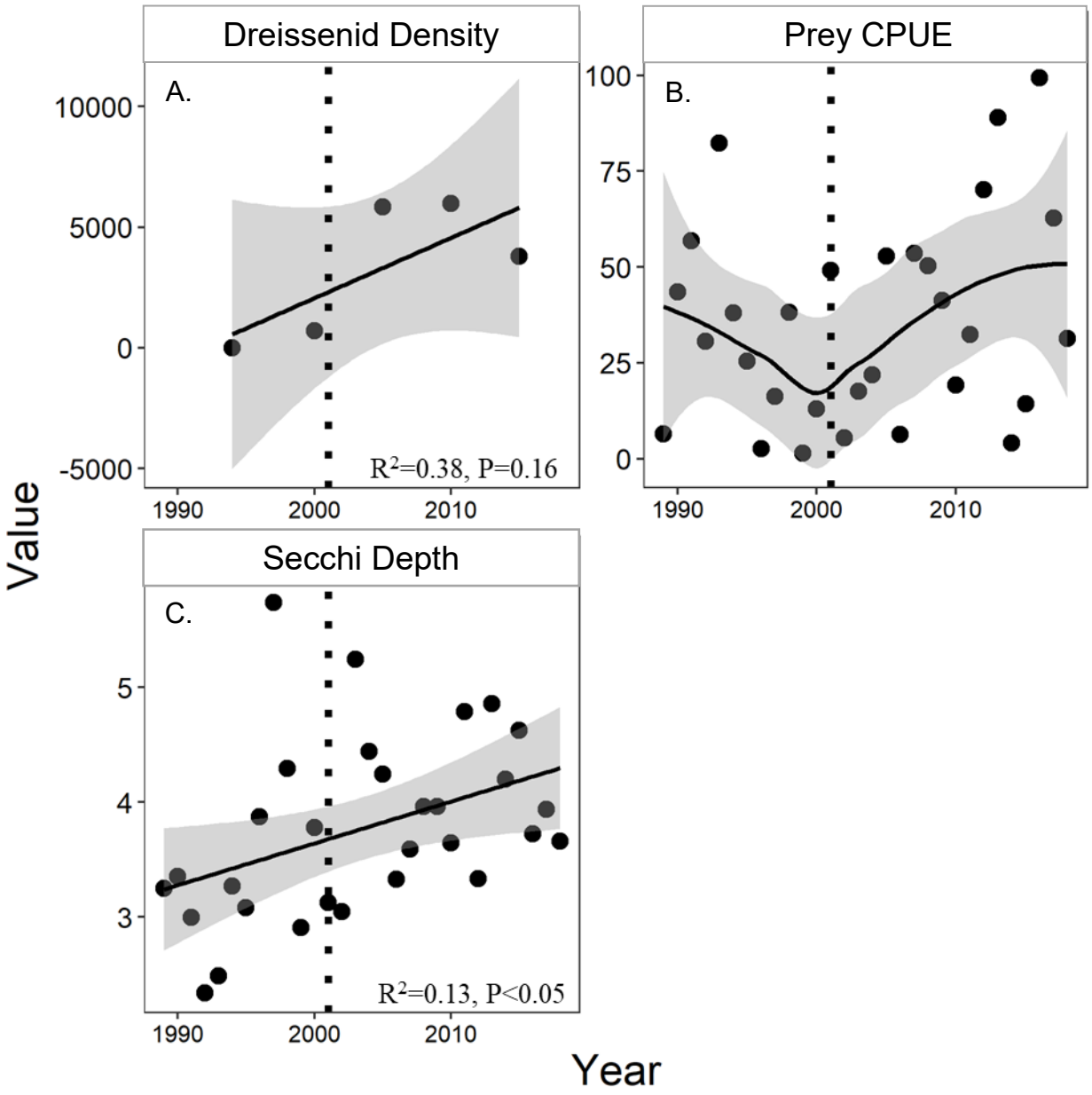

Figure 8. Temporal trends of environmental variables in LBdN (1989-2018). Trends in (A.) dreissenid density (no. /m^2) increased over time, (B.) prey CPUE declined until 2002 then increased due to the invasion of round goby, and (C.) secchi disk depth (m) displayed significantly positive relationship over time. Dashed red line indicates the separation in pre- and post-invasion periods (>2001).

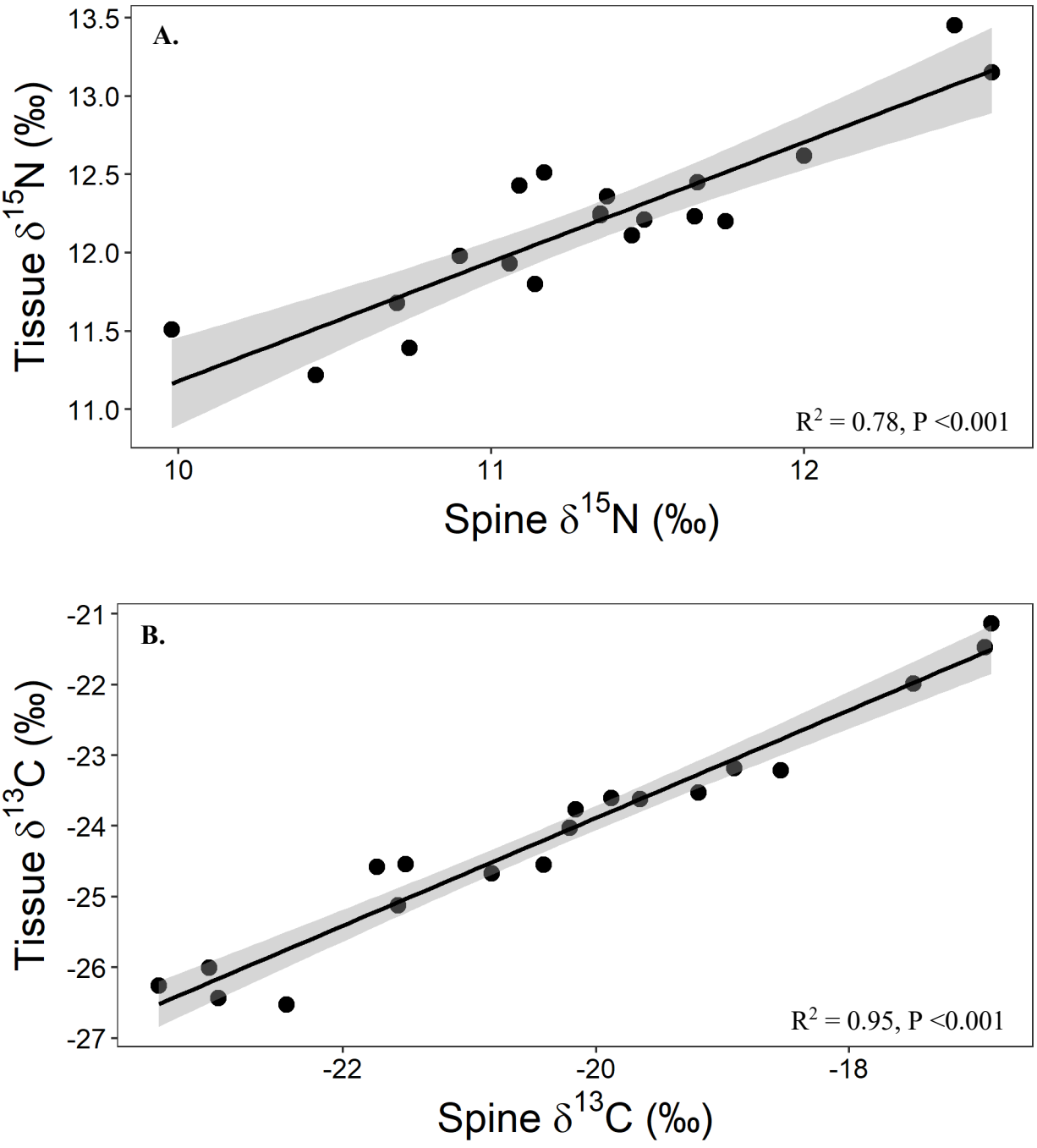

Figure 9. Spine and muscle tissue relationships for the stable isotopes of (A.) nitrogen and (B.) carbon. Isotope ratios of from these tissues were highly related allowing spines to be used as a proxy for muscle tissue in our archived samples using a correction factor.

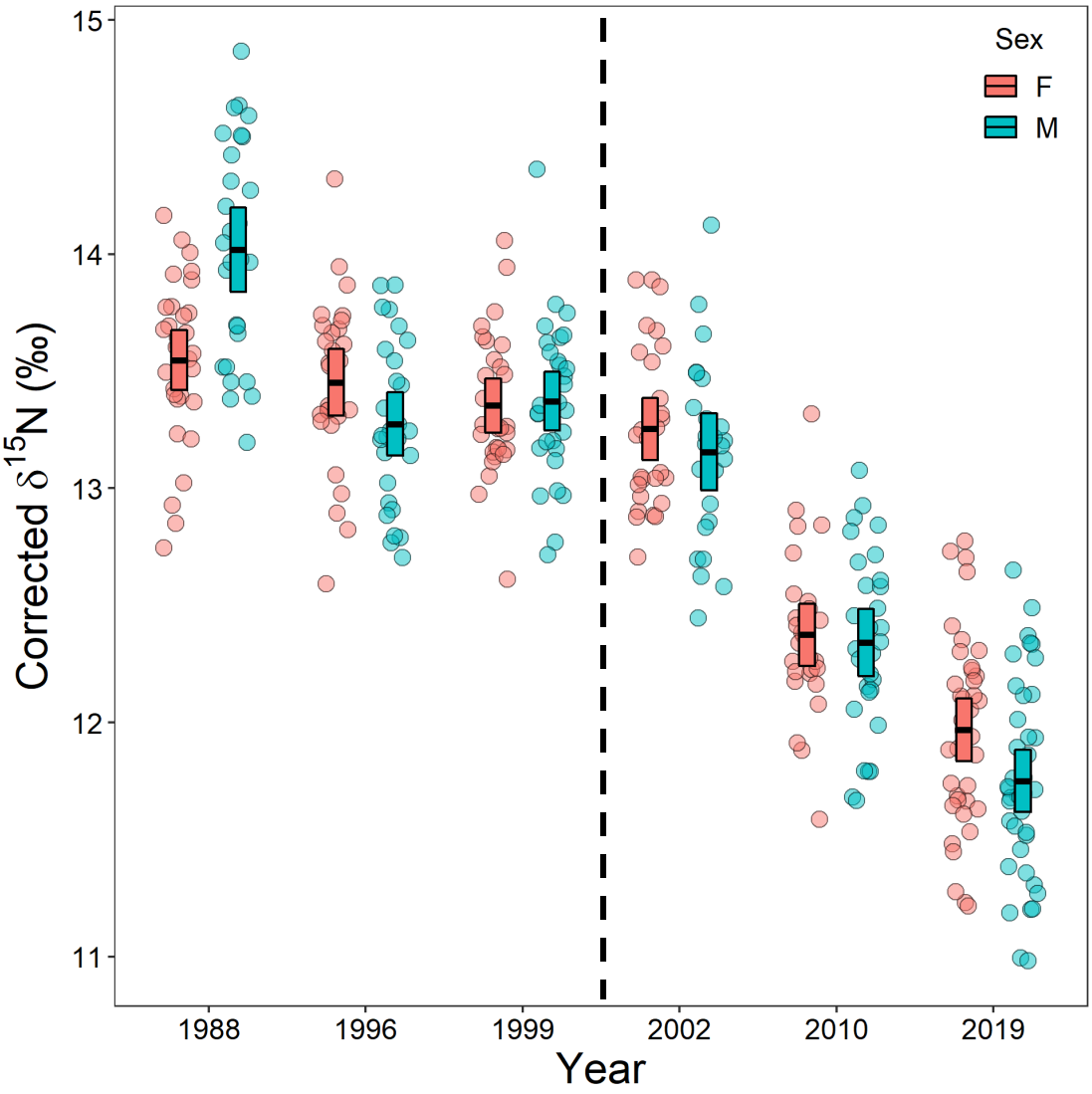

Figure 10. Sex-specific changes in $\delta^{15}N$ pre- and post dreissenid mussel invasion. Points represent isotope values of individual fish. The horizontal line indicates the sample mean while the top and bottom of the boxes represent the lower and upper Gaussian confidence limits based on the t-distribution. Overall, $\delta^{15}N$ declined ~1.1 ‰ in the post invasion period. Sex-specific differences within periods were much smaller in magnitude compared to differences between invasion periods. Dashed line separates pre- and post-invasion years. Note: a correction factor was applied to isotope values from archived spines and used as a proxy for dorsal muscle tissue for interpretation.

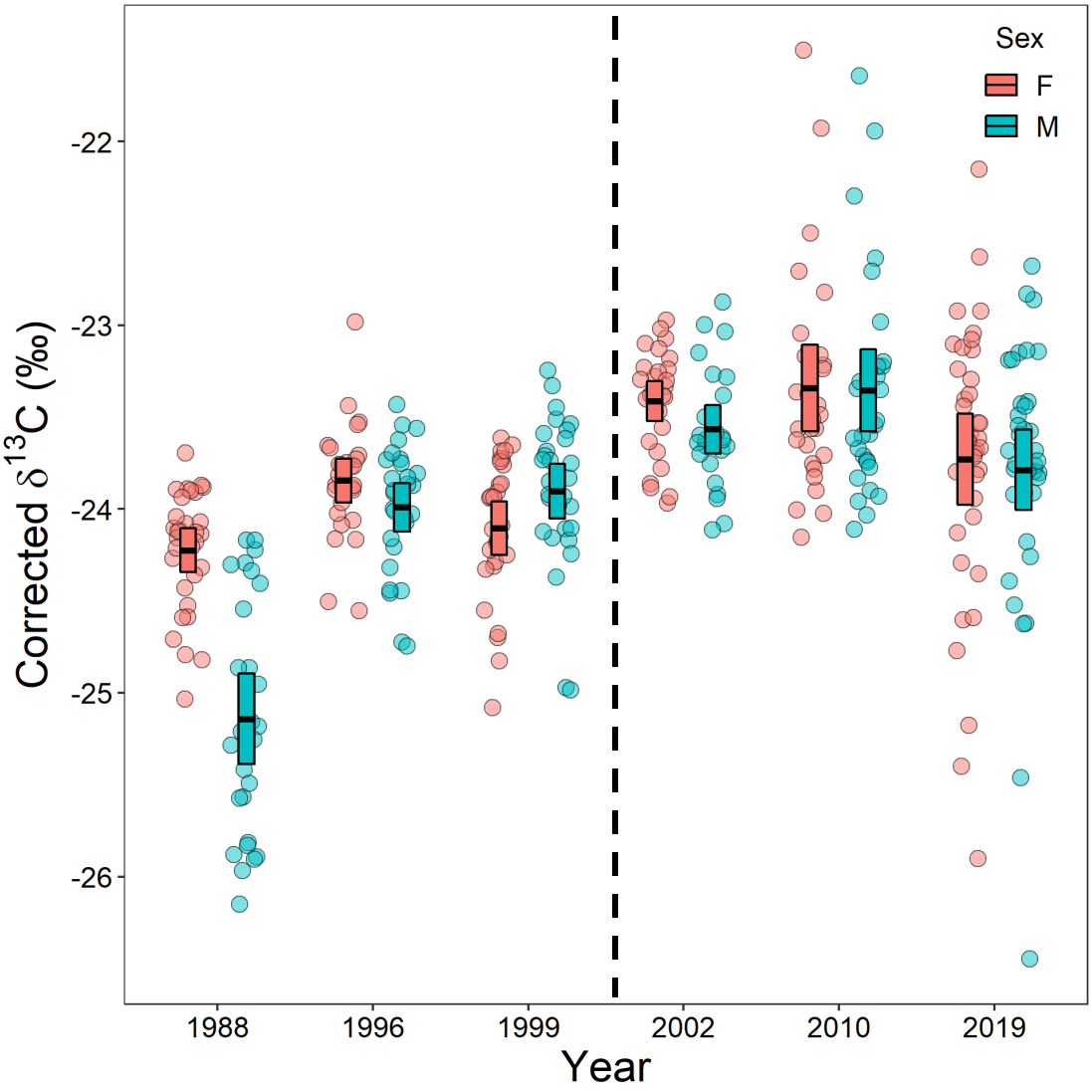

Figure 11. Sex-specific changes in $\delta^{13}C$ pre- and post dreissenid mussel invasion. Points represent isotope values of individual fish. The horizontal line indicates the sample mean while the top and bottom of the boxes represent the lower and upper Gaussian confidence limits based on the t-distribution. Overall, $\delta^{13}C$ increased ~1.2 ‰ in the post invasion period. Sex-specific differences within periods were much smaller in magnitude compared to differences between invasion periods. Dashed line separates pre- and post-invasion years. Note: a correction factor was applied to isotope values from archived spines and used as a proxy for dorsal muscle tissue for interpretation.

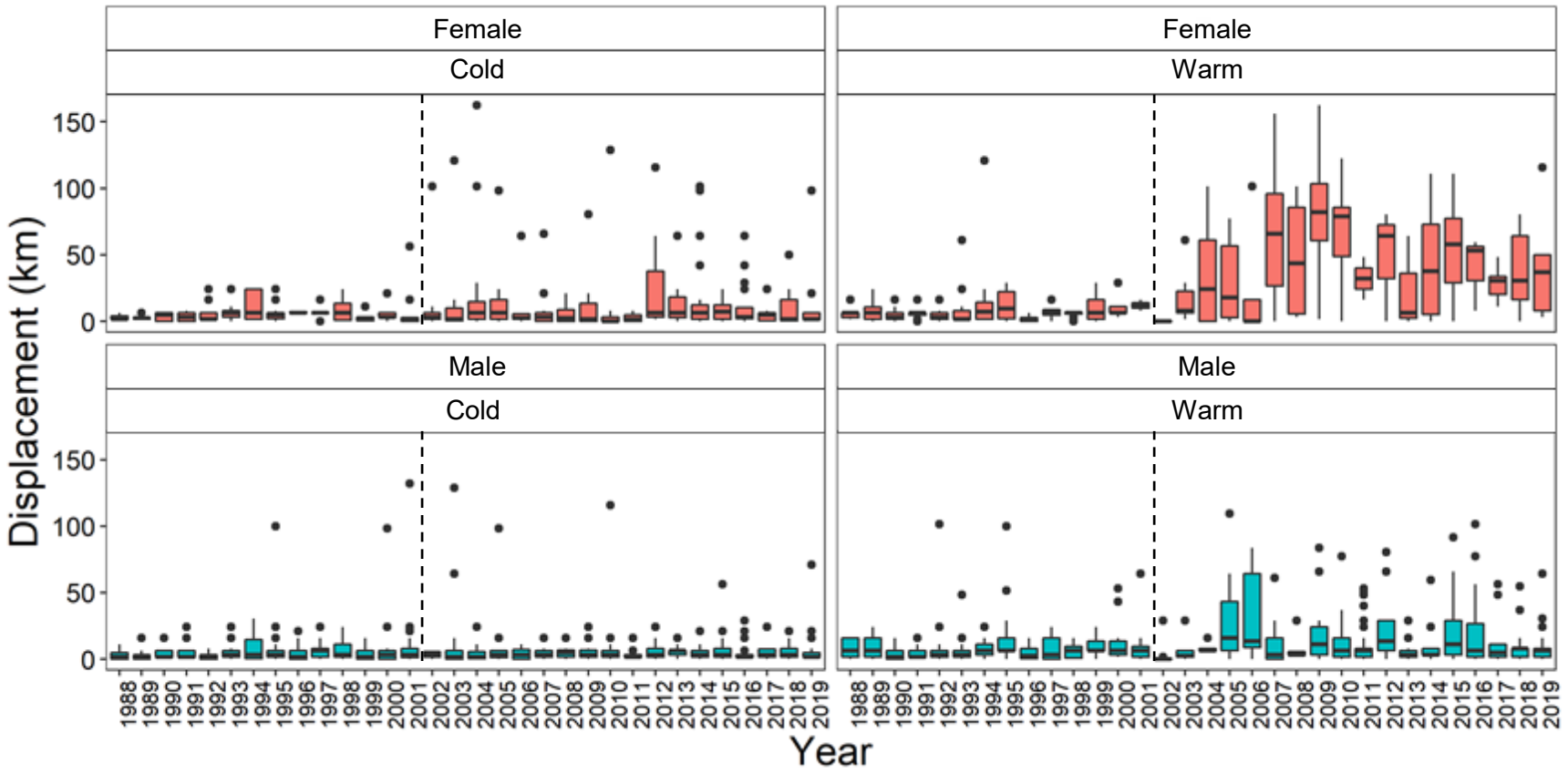

Figure 12. Box and whisker plots of sex-specific displacement distances from tagging location by invasion and return periods across a 31- year time series. Displacement was similar between males and females during the cold-water return period both pre- and post-invasion. In the warm-water return season, displacement was similar between the sexes during the pre-invasion period while female displacement was much greater than males post-invasion. Dashed line separates pre- and post-invasion years.

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